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Baltic cod recruitment – the role of physical forcing and species interactions

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Abstract

Reproductive success of cod in the Central Baltic depends on a suite of processes ultimately driven by climatic forcing. Egg survival which is dependent on oxygen and salinity concentration in dwelling depths of the permanent halocline, is thought to be the primary determinant of cod recruitment. Hydrographic conditions are affected by inflows of water from the Skagerrak/Kattegat and the western Baltic into the Central Baltic driven by special atmospheric forcing conditions. In this respect the horizontal distribution of cod spawning activity impacts on egg survival, as a considerable part of the egg production is spawned at certain years in areas of unfavourable environments not sustaining egg development. However, limited recruitment despite of favourable hydrographic conditions and sufficient egg production indicates that other processes are important, specifically egg predation by clupeids depending on the spatial overlap between predator and prey, as well as the availability of suitable food for early larvae hatching in deep Baltic basins, driven both by salinity and oxygen conditions in the halocline. In the present study we perform a retrospective analysis of the relative importance of these processes on recruitment success. The analysis is based on spatially dis-aggregated time-series of egg production and survival, standing stocks of larvae and juveniles, copepod prey availability and hydroclimatic variables. Finally, we discuss how identified primary processes affecting cod recruitment can be integrated into simple environmentally sensitive stock recruitment models.

Keywords: egg survival, Eastern Baltic cod, hydrography, larval prey availability, predation, recruitment

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Introduction

Climatic variability impacts on cod recruitment in the Central Baltic, inhabited by the so called Eastern Baltic cod stock. This has been demonstrated in a series of studies conducted throughout the last decades addressing especially egg developmental success (for review see Bagge *et al*., 1994 and Köster *et al.*, 2003a). In contrast to cod spawning areas outside the Baltic, the ambient salinity is insufficient to keep cod eggs floating in the surface layers. They occur exclusively within and below the permanent halocline (e.g. Wieland and Jarre-Teichmann, 1997). Here they are exposed to variable and in general low oxygen concentrations, suggesting a major impact of poor oxygen conditions on egg survival and subsequent recruitment success (e.g. Kosior and Netzel, 1989; Lablaika *et al*., 1989). Laboratory experiments confirmed that at least 2 ml/l oxygen concentration is needed for successful egg development (Nissling, 1994; Wieland *et al*., 1994). In estuarine systems, low salinity effects the fertilisation of marine fish species (Westin and Nissling, 1991). For Baltic cod, experimental studies revealed a minimum salinity of around 11 psu for activation of spermatozoa and thus successful fertilisation (Westin and Nissling, 1991). Both, the oxygen and the salinity threshold formed the basis for the definition of a 'reproductive volume', the water volume allowing for successful cod egg development (Plikshs *et al*., 1993; MacKenzie *et al*., 2000). The magnitude of the reproductive volume in the deep Baltic basins depends first of all on the frequency and the magnitude of inflows of saline water from the western Baltic, which in turn is related to atmospheric forcing conditions (MacKenzie *et al*., 2000) and secondly depends on oxygen consumption rates by biological processes (Hansson and Rudstam, 1990). However, also other processes impact on the quality of the cod spawning environment, e.g. temperature in the western Baltic during winter, affecting oxygen solubility prior to advection (for review see Hinrichsen *et al*., 2002a).

Although the reproductive volume has been successfully integrated into stock-recruitment relationships (Plikshs *et al*., 1993; Sparholt, 1996; Jarre-Teichmann *et al*., 2000), the amount of variance explained in recruitment is limited and especially the major Baltic inflow in 1993 did not increase the reproductive success as expected. This may have several reasons, firstly measurement errors in recruitment as dependent and spawner biomass as independent variables (with respect to Eastern Baltic cod, see Köster et al., 2003b) and methodological difficulties due to time series effects biasing parameter estimates (e.g. Walters and Collie, 1988). Secondly, the amount and quality of eggs produced by a unit of spawning stock biomass varies in Eastern Baltic cod significantly in relation to food availability

(Kraus *et al*., 2002) and stock structure (Vallin and Nissling, 2000). Thirdly, the reproductive volume may be not the best proxy for egg survival, as it does not consider egg mortality caused by low oxygen concentration above the threshold (Wieland *et al*., 1994), the possibility that eggs float outside the reproductive volume in water layers not sustaining their development (Köster *et al*., 2001a). Finally, other processes affect early life stage survival. Among these are food supply for larvae and early juveniles (Hinrichsen *et al*., 2002b), predation on cod eggs by clupeids (Köster and Möllmann, 2000) and cannibalism on juveniles (Sparholt, 1994).

The present contribution aims at disentangling the interactions between reproductive effort of the Eastern Baltic cod stock, climatic and hydrographic forcing conditions as well as species interactions. It will give an overview on the state of the art in Baltic cod recruitment research and tries to explain most recent and historic stock dynamics, with specific reference to the various processes affecting the reproductive success. It will point out gaps in our understanding and suggests actions to address them with the goal of establishing environmentally sensitive and spatially explicit stock recruitment models. To this end updated and simplified versions of the stock recruitment relationships suggested by Köster *et al*. (2001a) are presented.

Material and methods

Area disaggregated spawning stock abundance

Spawning stock biomass of the Eastern Baltic cod stock is estimated annually for the period since 1966 (ICES, 2003). These estimates are based on an XSA, tuned with catch rates from the first quarter international bottom trawl survey. Area dis-aggregated estimates for Sub-divisions (SD) 25, 26 and 28 (Fig. 1) are available from area dis-aggregated MSVPA runs (Köster *et al*., 2001b), here updated for the period 1976 to 1999 (for detailed information on technical set-up see ICES 2001a). Stock sizes were determined for the main spawning time, i.e. mid of May 1976-1990 and beginning of July 1991-1999, by this considering the shift in spawning time from spring to summer months (Wieland et al., 2000a). To estimate the basin specific female spawning stock biomass (assuming SD 25 to represent the Bornholm Basin, SD 26 the Gdansk Deep and SD 28 the Gotland Basin see Fig. 1), firstly sex ratios and female maturity ogives were applied to basin specific population abundances derived by area dis-aggregated MSVPA runs. Annual sex ratios and proportions of sexually mature individuals were utilised for SD 25 in 1988 to 1996 and for 26 in 1993 to 1996; otherwise 5 year averages were used (Tomkiewicz *et al*., 1997). For 1997 and 1998 corresponding values were reported by ICES (1998), while for 1999 an average over the period 1995 to 1997 was applied. Secondly weight at age as compiled in ICES (1999) and ICES (2001b) were utilised to convert the female spawning stock size into the corresponding biomass (SSB).

Potential egg production

To estimate basin specific seasonal potential egg production (PEP) by the spawning stock, female SSB according to Sub-division (SD) were multiplied by relative individual fecundity values. Utilisation of relative instead of absolute age-specific fecundity is justified by the fact, that this measure is independent of body size in Baltic cod (Kraus *et al*., 2000) and thus can be applied to the spawning

stock without considering the size/age structure. Relative fecundity for each SD was predicted from a relationship to clupeid prey availability (Kraus *et al*., 2002) applying MSVPA derived area specific abundances of clupeids as prey.

Egg and larval abundance

Mean annual egg and larval abundance values are available for the different spawning areas in SD 25, 26 and 28 from ichthyoplankton surveys conducted in the period 1966-1999. Egg abundance estimates are average of surveys conducted in a three-month period encompassing the main spawning period, i.e. April-June up to 1989 and successively shifted to mid April-July (1990), May-July (1991-1992), mid May-mid August (1993-1995) and mid June-mid September (1996 to 1999) corresponding to the peak spawning time as determined by Wieland et al. (2000a). Larval abundance data refer to a period similar to the three month period of egg abundance estimates, but shifted by one month to account for the period of development from egg to larvae (Wieland *et al.*, 1994).

Realised egg production and observed survival

Estimates of daily egg production at different developmental stages I to IV were derived on basis of stage specific egg abundance data from ichthyoplankton surveys and ambient temperatures from concurrent hydrographic measurements. Covered years and periods were 1974-1978, 1983, 1985-1999 for the Bornholm Basin, while for the Gdansk Deep and the Gotland Basin, the exercise was restricted to hydrographically contrasting years with best spatial coverage of the spawning areas, i.e. 1974, 1976, 1989 and 1995-1996. For the Bornholm Basin, the average stage specific abundance within a spawning season was computed by applying relative stage compositions averaged over usually 2-4 surveys conducted during the 3 month main spawning period to the average total egg abundance. Stage specific development times were determined on basis of: i) average temperature profiles in the Bornholm Basin from the ICES hydrographic database for the 2nd and 3rd quarter respectively, ii) mean egg dwelling depths as predicted from relative vertical distribution of cod eggs (see below) and iii) application of stage specific egg development-temperature relationships (Wieland, 1995). For the eastern spawning areas production values were calculated for single surveys only, applying temperature in the likely depths of highest cod egg concentration as recorded during the respective survey. Finally, the daily egg production was calculated by dividing the stage specific abundance by the development time of each egg stage. Non stage-able dead eggs were distributed to the different stages according to the relative stage-specific distribution of alive eggs, except for estimation of mortality rates (see below), when they were omitted.

Seasonal egg production rates in the Bornholm Basin were estimated for years being best covered with surveys and each survey adequately covering the spawning area, using date specific production rates of egg stages IA, IB, II and III. Stage IV was not considered in the computation, as hatching in Baltic cod occurs already in this stage (Wieland et al., 1994). The daily egg production per egg stage was estimated as described in Kraus et al. (2002). Applying differences in age between stages, these seasonal production values were utilised to calculate stage specific mortality rates per day and corresponding survival rates over the estimated developmental period.

In the period 1987-1993 and in 1999 repeated ichthyoplankton surveys in short time intervals (5-11 days) allowed the estimation of mortality rates from egg stage IA or IB to III by following daily production rates of specific egg cohorts applying the age difference between different stages (Wieland, 1995; Wieland *et al*., 2000b). In the case that mortality rates could only be determined for shorter developmental periods, i.e. from stages IA to IB or II and from II to III, an average daily mortality rate determined for these periods was applied to estimate survival until stage III.

Egg survival in relation of oxygen conditions

For estimating egg survival rates in relation to variable oxygen conditions, incubation experiments were conducted under controlled temperature conditions. The experimental set-up is described by Wieland *et al*. (1994) for the first series of experiments conducted in 1991/1992 and for the second series in 1995-1998 by Rohlf (1999), the latter with a slightly modified experimental set-up utilising a water re-circulation and not a flow through system. In all experiments egg batches from single females caught by trawling in the Bornholm Basin were fertilised by several males. Subsets of these egg batches were incubated at different oxygen concentrations and the viable hatch, i.e. larvae surviving through the yolk-sac stage, were expressed relative to the proportion surviving at normoxic conditions to separate the oxygen effect from other causes of mortality. A sigmoid survivorship function was fitted to the combined experimental dataset.

To estimate the fraction of cod egg production surviving during main spawning times in each year, the predicted vertical distribution of cod eggs in 5 m depth intervals relative to water density (see below) and the oxygen concentration at each depth interval derived from the ICES hydrographic database were coupled to the oxygen concentration/cod egg survival relationship derived from the incubation experiments. To model the vertical distribution of eggs, the observed distribution of the youngest egg stage (IA) obtained from vertically resolving ichthyoplankton sampling in April to July 1986-1996 was examined in relation to water density profiles by fitting a parabolic function to the log relative distribution data according to Köster et al. (2001a).

In the Bornholm Basin it has been observed that cod eggs are less buoyant after inflows when higher salinity occurs in the bottom water (Wieland and Jarre-Teichmann, 1997). Hence these hydrographic situations were modelled separately. Furthermore, upon inspection of the data, a seasonal effect in the vertical distribution of cod eggs was detected. Hence, the following yearly hydrographic and spawning situations were defined to group the data: a) stagnation/early spawning, b) stagnation/late spawning, c) inflow/early spawning and d) inflow/late spawning. For both other spawning areas in SD 26 and 28, the stagnation scenario was applied throughout the time series, as salinity values never exceeded the threshold set for the Bornholm Basin. However, the shift in spawning time was considered. As the current models do not take into account temperature, also known to affect the vertical distribution, a correction was made for low temperatures (< 1.7°C) by transferring the predicted relative abundance of eggs to the next deeper water layer (5 m intervals).

Reproductive volume and oxygen content

Estimates of the reproductive volume in different SDs were compiled by STORE (2003), and were taken for the period 1966-1973 directly from MacKenzie *et al*. (2000), assuming peak spawning to be in May, with the Kiel series applied for the Bornholm Basin. For the period 1976-1996, RV was adjusted to peak spawning time as presented by Köster et al. (2001a), while for remaining years Kiel estimates in the Bornholm Basin and updated Plikshs et al., (1993) estimates for the eastern basins were applied (ICES, 2004).

Egg predation by clupeids

Predation by sprat has a significant impact on cod egg survival in spring and early summer, while later in the cod spawning season herring is the principal predator (Köster and Möllmann, 2000). This seasonal shift in predator importance is caused by sprat concentrating in same deep water spawning areas as cod in spring and early summer leaving these areas in later summer, while herring return from their coastal spawning areas in early summer to their deep water feeding areas. As the population of herring is substantially lower than that of sprat, especially after the drastic increase in sprat stock size since the late 1980's, the overall predation pressure is lower in summer than in spring (Köster and Möllmann, 2000). Apart from intra-annual trends, spatial variation in the intensity of egg predation also occurs, with consumption in the Gdansk Deep and Gotland Basin being considerably lower than in the Bornholm Basin. For this reason, predation on cod eggs by clupeids was considered as mortality source for SD 25 only.

Cod egg predation intensity in the Bornholm Basin depends on the vertical overlap between predator and prey. Köster *et al*. (2001a) modelled the daily consumption of cod eggs by individual clupeids in spring and early summer as linearly related to cod egg abundance if the vertical predator/prey overlap is considered. This model is based on the observation that oxygen concentration in the bottom water limits the vertical distribution of clupeids during the daylight-feeding period, while the density regime determined the vertical distribution of cod eggs, with clupeids dwelling below cod eggs in inflow situations and in water layers with highest egg densities in stagnation years. Based on these observations, the average capture depth of the clupeids and the average depth in which highest concentrations of cod eggs occurred were combined into an index of vertical predator/prey overlap. In combination with daily egg consumption rates, predator populations sizes from area dis-aggregated MSVPA downscaled to the Bornholm Basin by historical hydroacoustic survey results and standing stocks of cod eggs, the predation pressure by clupeids populations on cod eggs was determined for the period 1976-1992 (Köster et al., 2001a). In the present analysis these estimates are updated by revised predator population estimates from new MSVPA runs and the predation pressure is expressed relative to the maximum value determined. This approach is limited to spring and early summer situations only, as sprat tend to leave the Bornholm Basin in summer (see above) and remaining individuals show a deviating vertical migration behaviour staying during day-time in the upper part of the halocline and the intermediate water while feeding on cladocerans (Köster and Möllmann, 2000). To accommodate for the shift we calculated observed average daily egg consumption per abundance

values for sprat and herring based on summer survey results 1994-1997 and applied these averages for 1993-1999.

Food availability for cod larvae

The major prey of first feeding cod larvae in the Baltic are calanoid copepod nauplii (Voss *et al*., 2003), specifically nauplii of *Pseudocalanus elongatus* (Hinrichsen et al., 2002b). The importance of P. *elongatus* nauplii for cod larval growth and survival was tested with a coupled hydrodynamic/trophodynamic individual based model of drift and feeding. Highly temporally and spatially resolved simulated flow fields were used to investigate the potential drift of Baltic larval cod from the centre of spawning effort in the Bornholm Basin towards their different nursery areas through temporally and spatially resolved idealized prey fields (Hinrichsen *et al*., 2002b). The idealised prey field included the dominant calanoid copepod (*P. elongatus*, *Acartia* spp., *T. longicornis*, *C. hamatus*) and cladoceran species (*B. longispina maritima*, *E. nordmanni*, *Podon* spp.) and refers to the 25-50m depths layer sampled with a vertical operated 160um Juday net. It was computed on basis of a zooplankton database compiled by the Latvian Fisheries Research Institute within the European Union-funded project "Baltic Sea System Study, BASYS". For detailed descriptions of the database as well as sampling and analysis procedures, see Dippner et al. (2000) and Möllmann et al. (2000).

In the present contribution, we discuss the results of the coupled hydrodynamic/trophodynamic individual based model with respect to the validity of the applied idealised prey field considering available independent data on zooplankton species and stock composition in the Bornholm Basin from i) Krajewska-Soltys and Linkowski (1994) covering three different stations in the 2nd and 3rd quarter 1991-1993 by water sampling in different depths layers, ii) from Hansen et al. (2004) covering April, May, June and August 1999 using a Bongo net with 150um mesh size for mesozooplankton equipped with a 50um liner for nauplii, and iii) displacement volumes from 335um Bongo samples from 32-45 stations covered at least two times in the 2nd and 3rd quarter 1988-1997 respectively.

Secondly, results of coupled model runs for 1999 (Hinrichsen *et al*., 2004) utilising measured prey fields from Hansen *et al*. (2004) are discussed. Furthermore, simulated larval survival rates are contrasted to observations by comparison with independent mortality measures derived by relating i) recruitment at age 0 (see below) to surviving egg production, either modelled as the product of PEP and OES or directly observed as average daily egg stage III production, and ii) recruitment at age 2 in the entire Central Baltic (year of origin) to the sum of PEP and OES over SDs. Finally, the nutritional status and protein growth rates of larvae sampled in 1994 and 1995 (Grønkjær *et al*., 1997), i.e. during a period of minimum larval survival, are reviewed.

Apart from prey availability and encounter, capture success may define larval feeding intensity. To accommodate this, the product of nauplii abundance during main spawning time and pursuit success were utilized as a measure of prey availability. Pursuit success probability has been calculated by utilizing a regression model for describing the influence of turbulent velocity on larval feeding success (MacKenzie and Kiørboe, 2000). This pursuit success model requires as input estimates of turbulent kinetic energy dissipation rate (from wind data time series) and prey separation distance (from prey

field data). Successful pursuit probabilities have been calculated for early (April-May), summer (June-July) as well as for later hatched larvae (August-September) for 30 m depths.

Recruitment

Estimates of age-group 2 recruitment for the entire eastern Baltic stock are available for the period since 1966 from regular stock assessments (ICES, 2003). Age-group 0 recruitment values for the different SDs were derived by area dis-aggregated MSVPA runs described above. The early juvenile stage was utilised instead of age-group 2 to minimise the effect of cannibalism (Uzars and Plikshs, 2000) on the perception of reproductive success.

Environmentally sensitive stock recruitment relationships

Based on results of conducted exploratory analyses and as an update of the study conducted by Köster et al. (2001a) following statistical stock recruitment models were constructed as simple multiple linear regressions for the different SDs (i):

$$R_i = a_i + b_i * PEP_i * OES_i + c_i * T_i * P_{p\ or\ n,i}$$

and the entire eastern Baltic stock as sum over SDs (model 1):

$$R = \sum \max(0,R_i)$$

alternatively model 2 directly fitted to all SD at once:

$$R = a + b * (\sum PEP_i * OES_i) + c * T * P_{p\ or\ n}$$

with:
- R_i: Recruitment at age 0 in SD i
- PEP_i: Potential egg production in SD i
- OES_i: Oxygen related egg survival fraction in SD i
- T: pursuit success during and after peak spawning time
- $P_{p\ or\ n}$: prey availability as *P. elongatus* or total nauplii abundance per m^3 (entire water column during 2nd quarter until 1990 and 3rd quarter 1991-1999 as average over SD 26 and 28)
- a, b, c: estimated parameters

The statistical models were fitted to data covering the period 1976-1999. Excluding data for 1974-1975 is justified by the uncertainty of MSVPA input data for these years (ICES 2001a).

Results

Hydrographic conditions in spawning areas

The hydrographic conditions in the deep Baltic basins are characterised by a permanent halocline separating the intermediate cold water layer, formed in winter by vertical convection, from the saline bottom water layer, created by regular intrusion of water from the western Baltic and occasionally larger Baltic inflows. In spring/early summer a thermocline develops in upper water layers separating a warm water surface layer from the intermediate water (Fig. 2-4).

Cod eggs are neutrally buoyant within and below the halocline (e.g. Wieland and Jarre-Teichmann, 1997), while cod larvae migrate at the end of the yolk-sac stage upwards into the intermediate water

with preference for depths below the thermocline (Grønkjær and Wieland, 1997; Rohlf, 1999). While the depth of the thermocline is relatively similar in all basins, the depth and extension of the halocline is not. It is in general shallower and has steeper salinity gradients in the Bornholm Basin with intermediate features in the Gdansk Deep.

The hydrography in the Bornholm Basin during cod spawning time (Fig. 2) is characterised by a high variability in oxygen concentration in bottom waters caused by regular inflow events, i.e. in 1969, 1972, 1976, 1979, 1980, 1985, 1986 and 1991-1993. However, only inflows in the first half of the time series introduced highly saline water as well; an exception is 1993. Inflows situations are in general related to relatively low bottom water temperatures as the inflown water originates from well mixed near surface layers in the western Baltic during winter. The increase in temperature in surface water layers visible during the 1990's is related first of all to a shift of spawning time of cod to summer month, but also a general increase in water temperature, detectable as well in the bottom water (Fig. 2). Major inflow situation normally resulted in a rise of the halocline, still visible also in years after the inflow happened.

The hydrography in the Gdansk Deep (Fig. 3) is characterised by only 4 situations with oxygen concentrations of >3 ml/l at the bottom, i.e. in 1976, 1983, 1990 and 1991. These relatively high oxygen concentrations are not accompanied by high salinities, which occurred at other occasions, e.g. in 1970 and 1975.

The Gotland Basin shows indications of a long term freshening with declining isohalines from mid 1970's to 1994, i.e. a decline of the 11 PSU isohaline from 100 to 200 m (Fig. 4). Although this deepening of the halocline allows the vertical convection in winter to oxygenate lower water layers, oxygen concentrations below 100 m were in general <2 ml/l, with the exception of 1994, when an inflow introduced large quantities of water with oxygen concentrations >3 ml/l. Due to relatively high salinity the inflowing water replaced part of the anoxic water layers, resulting in an intermediate oxygen depleted water layer. Not only in this case, but also in general the Gotland Basin shows the least favourable conditions for successful cod egg production.

Potential egg production in different spawning areas

The potential egg production by the cod stock (PEP) follows in general the trend of SSB as determined by the regular stock assessment with a maximum in the early 1980's, a sharp decline during the 2nd half of the 1980's and a minor peak in the mid 1990'ies. The changes in reproductive potential are, however, more pronounced in PEP than perceived from the SSB development (Fig. 5a). The high PEP in the early 1980's results from high egg production in all three spawning areas, while a second peak in the 1990's is primarily due to spawning in SD 25 with the egg reproduction in SD 28 being extremely low since the late 1980'ies.

The reproductive volume and it's utilisation as spawning habitat

Comparing the PEP with the reproductive volume (RV) at spawning time, suggests that a large portion of the egg production in the Gotland Basin has been spawned in unsuitable environments in the late 1970's and early 1980's, when the cod stock was on a high level (Fig. 5a and b). Since the early 1980's hydrographic conditions were also adverse in the Gdansk Deep. Especially from 1986-1992

virtually no RV was present in both eastern spawning areas. The only area regularly sustaining a successful egg development was the Bornholm Basin. As a consequence of the major Baltic inflow in 1993 (Matthäus and Lass, 1995), oxygen concentrations allowed successful egg development in the Gdansk Deep in 1993 and 1994, and resulted in one of the highest RV on record in the Gotland Basin in 1994. While a substantial PEP was estimated in the Gdansk Deep, the corresponding production in the Gotland Basin was on a very low level. However, even a substantial egg production in the Gotland area in 1994, would likely not have resulted in high egg survival, as the salinity in the oxygen depleted intermediate water layer was high enough to keep a large fraction of the eggs floating, but having insufficient oxygen concentration for successful development.

Egg survival in relation to oxygen concentration

The influence of oxygen concentration on the proportion of viable hatch derived from controlled laboratory experiments showed that oxygen concentrations above the threshold level of 2 ml * l^{-1} utilised in the definition of the RV, still have a pronounced impact on the egg survival (Fig. 6). At about 4 ml * l^{-1} only half of the egg production survives. In order to apply the fitted sigmoid oxygen – egg survival relationship (r^2 = 0.95) to estimate the fraction of the egg production surviving in each spawning season, the vertical distribution of the youngest egg stage IA was modelled in relation to the ambient density. The explained variance in these vertical distribution models ranged between 72 and 82% for the four environmental scenarios considered, with the least explained variability for the inflow/spring spawning scenario. Coupling predicted vertical distributions, measured oxygen concentrations from the ICES hydrographic database and the laboratory derived survival relationship revealed a time series of modelled oxygen related egg survival fractions (OES) for each SD (Fig. 5c). The OES values indicate that egg survival was always by highest, though variable, in the Bornholm Basin, while egg survival especially in SD 28 has always been low. This result does not coincide with relatively high egg and larval abundance values in the 1970's up to mid 1980's in all three basins derived by ichthyoplankton surveys (Fig. 5d and e). This inconsistency is as well obvious for the reproductive volume indicating sufficient hydrographic conditions for egg survival only in very few years (Fig. 5b).

To validate the OES and the RV as measures of egg survival, the realised egg production at stage III as derived from ichthyoplankton surveys in the Bornholm Basin was regressed on the PEP, with and without multiplying PEP with OES and adding RV as additional variable. While the latter decreased the explained variance (r^2=0.58) compared to the simple model utilising only PEP (r^2=0.61), multiplying the PEP with the OES increased the r^2 to 0.73 (Fig. 7). A large negative residual was encountered in 1983, when the observed egg stage III production was considerably lower than predicted from the PEP and egg survival, while 1976 and 1994 behaved in an opposite way.

The OES compares favourable to the egg survival as determined by successive ichthyoplankton surveys in corresponding years (Fig. 8a, r^2=0.64). A linear regression of the observed on the predicted survival until egg stage III has a slope of 0.41 (p=0.01) (intercept insignificant), indicating that other mortality causes than oxygen depletion affect egg development success. Although egg survival derived

from seasonal egg production curves and cohort development are closely related (r^2 = 0.82, n = 8), the relationship between OES and egg survival from seasonal production curves is less satisfactory (r^2 = 0.36, p = 0.153, n = 7). This is explained by large residuals in 1991 and especially 1996, with a high predicted and a low observed survival (Fig. 8b). The latter deviation does not enter the comparison to the survival from cohort development (Fig. 8a), as in 1996 no repeated ichthyoplankton surveys were performed. Interestingly the highest predicted and observed egg survival was encountered in 1993 and 1994, despite that resulting larval abundance was low in these years (Fig. 5e).

Average daily egg mortality rates in different spawning areas are compared in Tab. 1 for contrasting environmental conditions. Egg mortality rates were relatively low in 1974 and 1976, with the exception of the Gotland Basin showing in the latter year an intermediate value. These years can be considered as typical inflow years with in general high RV (with the exception of 1974 in SD28) and as well relatively high OES (Fig. 5c). Differences in mortality rates between the different areas are, however, not consistent with the oxygen related egg survival according to which the egg mortality should have been lowest in the Bornholm Basin. While this is the case in 1976, mortality was lowest in 1974 in the Gdansk Deep (Tab. 1). In a typical stagnation year, 1989, egg mortalities were relatively low only in the Bornholm Basin, but extremely high in the eastern spawning areas, consistent with the expectations. In 1995 and 1996, years being characterised by relatively favourable conditions in the Bornholm Basin, egg mortality rates were again relatively low in this area, while they were very high in the Gotland Basin (data from the Gdansk Deep missing). Variability in egg mortality rates determined for the Bornholm Basin are not associated to variability in RV and OES, which again may indicate other processes affecting egg mortality.

Egg predation by clupeids

The total daily consumption of cod eggs by sprat and herring populations in the Bornholm Basin during main spawning periods 1990-1997 are presented in Fig. 9a. Comparing the daily egg consumption rates by both predator populations with daily production rates and standing stocks of cod eggs in the area confirmed a high predation by sprat in early 1990's when the cod spawning season was still in spring and early summer. In fact predation was estimated to be above daily production and standing stocks in 1990-1992 and above the production in 1993. After the shift of cod spawning activity into summer, predation by herring increased to 50 to >100% of the daily production and up to 50% of the standing stocks. Somewhat outstanding is the relatively high predation by sprat in summer 1997 reaching a similar value as determined for herring (Fig. 9a).

Assuming these consumption estimates to be unrealistic high, and expressing the predation pressure in relative terms, i.e. as ratio of daily consumption to production scaled to the maximum value determined for sprat in spring 1992, revealed a clear minimum of egg predation in 1993-1995. This can be explained by a combination of limited vertical overlap between predator and prey after the 1993 major inflow event and the shift of cod spawning time into summer. The effect of the shift in spawning time can be inferred from comparison of the relative predation pressure during May/June and July/August 1994-1997 respectively (Fig. 9b). The predation pressure by sprat was approximately 2.5

times higher in spring/early summer than later in the years, while the predation pressure by herring was approximately 8 times higher in summer than in spring. The effect of the vertical predator – prey overlap can be deduced form comparing values for May/June 1990-1992 to 1993-1996. Sprat and herring predation reduced by a factor of 6 and 3.5 respectively. Focussing on the individual consumption by comparing mean daily rations of cod eggs by individual sprat and herring per egg abundance (Fig. 9c), confirms that the individual egg predation by sprat follows closely the predator prey overlap (Fig. 9d), while the relationship is less obvious for herring.

Comparing the oxygen related egg mortality during stomach sampling cruises as inferred by vertical resolving plankton sampling, hydrographic measurements and application of the oxygen concentration – egg survival relationship (Fig. 6) revealed a similar trend in hydrography induced egg mortality and predator/prey overlap (Fig. 9d) and hence predation pressure as well. This can be explained by the fact that the same hydrographic parameters affect the vertical predator/prey overlap and oxygen related egg mortality, i.e. salinity and oxygen concentration. This is also obvious from a comparison of modelled relative predation pressure and oxygen related egg survival (OES) for the period until mid 1990's (Fig. 10), while deviations in most recent years are caused by the shift of cod spawning time from spring to summer.

From egg to the larval stage

The abundance of cod eggs during main spawning time was in general highest in the Bornholm Basin, with a considerable interannual variability especially in the Gdansk Deep and the Gotland Basin and a decreasing trend in all areas throughout the 1980's (Fig. 5d). Since 1986 the contribution of the eastern spawning areas were marginal, in fact much less than indicated by the potential egg production estimates at least in the Gdansk Deep. In summary, egg abundance values indicate either low spawning activity in eastern spawning areas since mid 1980's, or extremely high egg mortality rates, e.g. salinities not allowing eggs to float in the water column.

In line with this observation, cod larvae were regularly encountered after 1985 only in the Bornholm Basin, but in relatively low abundances (Fig. 5e). In fact, despite historically high egg abundance values encountered in 1994 to 1996 (Fig. 5d), high modelled egg survival in 1993-1996 (Fig. 10) and high observed egg survival at least in 1993/1994 (Fig. 8), larval abundance was comparatively low in all these years (Fig 5e). This indicates high mortality rates in the early larval stage, which has been explained by a limitation in food availability for first feeding larvae (see below).

Larval survival in relation to food availability

Investigating the impact of food availability on growth and survival of cod larvae with a coupled hydro/trophodynamic individual based model (Hinrichsen et al. 2002b) revealed i) a food limitation of first feeding cod larvae since in the 1990's, caused mainly by a decline in the abundance of the calanoid copepod *P. elongatus* and ii) retention and dispersal from the main spawning ground to be a key process influencing larval survival. When *P. elongatus* was available in the prey fields, food limitation occurred only late in the spawning season (Fig. 11a). When *P. elongatus* was not available larval survival probabilities were higher in the beginning and the end of the spawning season (Fig.

11a). Higher survival early in the spawning season is caused in the model by on average lower temperatures (Fig. 11b) and related lower food requirements for sustaining standard metabolism. Relatively high survival later in the spawning season is coupled to an increasing nauplii production by other calanoid copepods and enhanced transport into productive shallow water areas. Inter-annual variability in larval survival from peak spawning activity as derived by coupled model runs under as realistic as possible prey availability (Hinrichsen et al., 2002b) suggests a low survival from 1993-1997, with the exception of 1996 (Fig. 12). The latter can be explained by relatively high wind speeds (affecting transport and prey encounter via turbulence), below average temperatures (Fig. 2) and relatively high *P. elongatus* availability (Fig.13b).

Low survival through the larval stage in mid 1990's was already indicated by the ratio of egg to larval abundance encountered in the Bornholm Basin (Fig. 5d and e) and is confirmed by relating 0-group recruitment to different measures of surviving egg production (Fig. 12). Simulated and observed larval survival rates were lowest from 1993-1995, a period of favourable oxygen conditions for egg survival (see above). Before 1992 observed survival rates were in general lower and more variable than the coupled model output, indicating other larval or early juvenile mortality sources. Despite the general agreement of simulated and observed low larval survival in the mid 1990's, the relatively high larval survival suggested by the model for 1996 is not confirmed by any of the observations.

Running the model with measured prey fields in the Bornholm Basin for 1999 revealed that food supply for cod larvae was sufficient for early hatched individuals, whereas the late hatched survivors had to be transported to coastal areas (Hinrichsen *et al*., 2004). No starvation mortality occurred for individuals spawned in April and May, whereas survival of larvae hatching in June to August 1999 decreased to about 60%. This result leads to the question whether the food supply improved from mid to end 1990's or whether the idealised prey field used in the coupled model was underestimating the prey availability. The vertical integrated *P. elongatus* abundance measured in 1999, being the basis of a vertically resolved prey field used in the run for 1999, was very similar to the values determined for the eastern basins in spring and summer 1999 (Fig. 13a). Polish investigations covering the Bornholm Basin in 1991-1993, determined somewhat higher *P. elongatus* nauplii abundance (Krajewska-Soltys and Linkowski, 1994), however being in spring well below the average *P. elongatus* abundance in the Latvian time series being basis for construction of the idealised prey field utilised in the simulations (Fig. 13a). In contrast *P. elongatus* nauplii abundance in summer was above the long-term average of the Latvian data series (Fig. 13b) and this is in fact also true for the nauplii of the other, smaller copepods. All presented data show a decline in prey availability from early to mid 1990's. This includes displacement volumes, measured on a high number of stations from 1988 to 1997, showing a highly significant reduction in mesoozooplankton biomass from 1991 to 1995 (Fig. 13a). Apart from this, a relatively high survival from main spawning activity in 1999 as indicated from the coupled model simulations is confirmed by available observations on survival from late egg production to recruitment (Fig. 12).

From larval to juvenile stage

Significant relationships exist between larval abundance and recruitment at age 0 in SD 25 and 26 (SD 25: $p=0.002$ and $r^2=0.33$, SD 26: $p<0.0001$ and $r^2=0.49$). In SD 28 and to a lesser extend also in SD 26 recruitment is encountered regularly despite the absence of larvae in the ichthyoplankton surveys (Fig. 5e and f). Comparing the time series of cod larval abundance in the Central Baltic, i.e. the integrated abundance in all spawning areas which should be unaffected by transport between spawning areas, with recruitment from the standard assessment revealed a highly significant relationship $p<0.0001$ and $r^2=0.53$. This does however not imply that mortality from the larval to the early juvenile stage is constant. On the contrary, high larval abundance observed in all spawning areas in 1984/1985 did not result in outstanding recruitment, indicating situations with higher than normal mortalities at the early juvenile stage. A mortality source of significance in juvenile cod is cannibalism (Sparholt 1994), which is however accounted for in the present analysis, as 0-group abundance from MSVPA runs are used. According to Neuenfeldt and Köster (2000), recruitment estimates from MSVPA runs are affected by the choice of the suitability submodel (standard according to ICES, 1992 or suggested by Gislason and Sparre, 1987) and whether a suitability model estimating suitability coefficients is used at all. Suitability coefficients may be interpreted as being proportional to the probability of encounter of predator and prey multiplied by the probability of the predator eating the prey once encountered, and the present assumption in the MSVPA is that these coefficients are prey age, quarter and area specific, but constant between years. Juvenile cod abundance (age 1) and cannibalism rates as determined by MSVPA runs using the two different suitability models under discussion and based only on observed stomach contents available for 1977-1993 are presented in Fig. 14. Deviations in recruitment estimates are obvious for the beginning of the time series, with the MSVPA without suitability modelling suggesting highest recruitment for year-classes 1976 and 1977, while otherwise highest year-classes are 1979 and 1980. The former result fits better to the larval abundance (Fig. 5e), indicating that the 1977 year-class may be under- and the 1980 year-class overestimated by the present MSVPA runs (Fig. 5f). However, the relatively low recruitment success in 1984 and 1985, despite high larval abundance, cannot be explained by underestimating cannibalism. Recruitment at age 2 as obtained from the XSA suggests in fact higher recruitment originated in these years, a deviation obvious also for 1991, although less pronounced (Fig. 5f).

Environmentally sensitive stock recruitment relationships

Relating surviving egg production, i.e. the potential egg production corrected for oxygen related egg survival (PEP * OES), and prey availability for first feeding larvae, i.e. the product of pursuit success (T) and *P. elongatus* nauplii abundance (P_p), as variables into a multiple linear regression revealed highly significant relationships in all SDs, explaining between 69 and 73% of the variability in recruitment. From the parameter estimates it is obvious that the impact of oxygen related egg survival increases from SD 25 to 26 and 28, while the impact of prey availability decreases (Tab. 2). Utilizing the total nauplii abundance (P_n) instead of the *P. elongatus* nauplii abundance improved the multiple regressions models slightly, explaining between 71 and 75% of the recruitment variability in the

different SDs and confirmed the trend in parameter estimates (Tab. 2). Autocorrelation in the residuals was indicated by the DW statistics especially for SD 26.

Constructing a single model for the entire eastern Baltic stock (model 2) is as well highly significant (Tab. 2, r^2 = 0.73) with a slight trend for autocorrelated residuals (DW = 1.15) underestimating the recruitment in the beginning of the time series (Fig. 15). This trend is even more pronounced when replacing P_p by P_n (DW = 0.97), though the explained variance is slightly higher (r^2 = 0.76). Predicting recruitment for single SDs and then integrating the results (model 1) with *P. elongatus* nauplii representing prey availability, explained 78% of the variance in recruitment at age 0. This somewhat better performance in compassion to model 2 was to be expected as the integrated model is based on more parameters.

Discussion

Hydrographic conditions in spawning areas

The hydrographic conditions in the central Baltic allow a regular successful reproduction of cod only in the Bornholm Basin (MacKenzie *et al*., 2000; Köster *et al*., 2001a). According to Hinrichsen et al. (2002a), processes affecting the reproductive conditions are: i) the magnitude of inflows of saline water from the western Baltic, ii) temperature regimes in the western Baltic during winter affecting the oxygen solubility prior to advection (which normally takes place during winter months, Matthäus and Franck, 1992), iii) river runoff into the Central Baltic and iv) oxygen consumption by biological processes.

While regular minor inflows and leakages from the western Baltic introduce saline and oxygenated water into the Bornholm Basin, only substantial inflow events improve reproductive conditions in the Gdansk Deep and especially the Gotland Basin. As the Baltic is characterised by a series of deep basins separated by shallow sills, a regular minor inflow will usually fill up the first basin (the Bornholm Basin) only, with little or no transport in eastern direction. Only if the inflow has a substantial magnitude or if the advected water is replaced by an even denser water mass in a subsequent inflow or a subsequent inflow of less dense water glides over the earlier inflown water, the eastern Baltic basins will benefit from the water exchange. The duration between a detection of these inflow events in the Bornholm Basin and in the Gotland Basin is in minimum 4-5 months up to nearly a year (ICES, 2004). This explains why the reproductive conditions in the different spawning areas are not necessarily in phase, i.e. may substantially vary within a spawning season.

Inflow events in the eastern basins, do not necessarily improve reproductive conditions. An example is the inflow in 1993 reaching the bottom water of the Gotland Basin in 1994. However, due to a relatively high salinity the inflowing water replaced part of the anoxic water layers in great depths, resulting in an intermediate oxygen depleted water layer having sufficient salinities to keep cod eggs floating, but insufficient oxygen concentrations to sustain their development (Plikshs et al., 1999).

Utilisation of spawning habitats

A comparison of the potential egg production (PEP) in the three spawning grounds with the reproductive volume at spawning time, suggests that during late 1970's and early 1980's a large

portion of the egg production has been spawned in unsuitable environments in the Gotland Basin and during the 1980's in the Gdansk Deep. The PEP depends on the distribution of the adult stock derived from area dis-aggregated MSVPA runs and ultimately on the distribution of catches in the different SDs (Köster *et al*., 2001b). Thus, the MSVPA output reflects rather the overall distribution of the stock throughout the year than at spawning time and may be sensitive to spawning migrations from eastern areas into the Bornholm Basin, having normally the best hydrographic conditions for reproduction. To test for a potential spawning migration, Tomkiewicz and Köster (1999) conducted bentho-pelagic trawl surveys on major spawning grounds from February/March to August 1996. While catch rates of adult cod in the Gdansk Deep and the Gotland Basin decreased throughout spring until peak spawning time in July/August, they increased in the Bornholm Basin, indicating a spawning immigration from eastern areas into the Bornholm Basin. This finding confirms earlier investigations based on tagging experiments (Netzel, 1974) and analysis of commercial CPUE data (Lablaika and Lishev, 1961) indicating spawning migrations to the Bornholm Basin in dependence of hydrographic conditions in eastern spawning areas. These spawning migrations explain part of the deviation between the large-scale horizontal SSB distribution from 1st and 4th quarter trawl surveys and from area dis-aggregated MSVPA (Köster *et al*., 2001b). On the other hand, Kraus *et al*. (2002) demonstrated for the Bornholm Basin highly significant relationships between the PEP and realised daily egg production estimates from ichthyoplankton surveys, indicating only limited influence of from year to year variable spawning migrations on the PEP. In combination with reports on pelagic pre-spawning and spawning concentrations in the Gotland Basin (Uzars *et al*., 1991) and presented egg abundance data for the eastern spawning areas, the conclusion appears to be valid that large-scale spawning effort took place in eastern spawning areas, despite at times unfavourable hydrographic conditions. Consequently, a mis-match of reproductive effort and spawning habitat quality was one of the main causes of declining reproductive success and recruitment failure of the stock during the 1980's.

Egg survival in relation to oxygen concentration

The established oxygen concentration – egg survival relationship combines data from Wieland *et al*. (1994) and Rohlf (1999), who utilised a similar technical and experimental design for their incubation experiments. The minor technical modification introduced in the second series of incubation experiments is not expected to affect survival rates determined, in particular not because relative viable hatch is used in order to eliminate a possible bias due to the different experimental set-up. The experiments confirmed that below 2 ml * l^{-1} oxygen concentration no successful egg development occurs, thus validating the oxygen threshold utilised in the definition of the RV. However, the results clearly indicate that survival success above this threshold depends still on oxygen concentration, as earlier reported by Wieland *et al*. (1994). When fitting the sigmoid oxygen egg survival model, we decided to keep three parameters including a = 1.0808, which in fact allows adjusted relative viable hatch > 1.0 as observed in the experiments. We however, truncated egg survival in the modelling approach at 1.0.

In the presented analysis an oxygen related egg survival factor (OES) replaces the reproductive volume (RV) or the sum of oxygen in the reproductive volume (ORV) utilised before to explain interannual variability in egg survival and recruitment success (Plikshs *et al*., 1993; Sparholt, 1996; Jarre-Teichmann *et al*., 2000; Köster *et al*., 2001a). As prerequisite for the development of the OES, the vertical distribution of cod eggs has been predicted for different environmental scenarios, i.e. early and late spawning as well as stagnation and inflow situations. The latter differentiation accounts for the observation that the buoyancy of cod eggs in the Baltic is reduced when ripening of adults and release of eggs takes place at increased salinities (Wieland and Jarre-Teichmann, 1997). A dependence of egg buoyancy on the timing of peak spawning is difficult to explain at present. Furthermore, the low survival rates derived for the eastern spawning areas are somewhat astonishing. Egg survival rates determined under favourable hydrographic conditions in the Gdansk Deep and the Gotland Basin in 1974 and 1976 by ichthyoplankton surveys are much higher than suggest by the OES. Ichthyoplankton surveys are of course sensitive to a loss of newly spawned eggs from the water column due to insufficient buoyancy. The applied method implicitly assumes that the entire egg production is able to float and that dead eggs dissolve beyond stage identification or sink to the bottom rapidly. According to the applied vertical distribution model only 6-37% of the eggs produced were able to obtain neutral buoyancy in the Gdansk Deep, while the percentage in the Gotland Basin was higher, i.e. 22-52%, due to the greater depths of the basin. As the hydrographic conditions in the bottom water of the Gotland Basin is less favourable than in the Gdansk Deep this does, however, not translate into a higher estimated egg survival. It does as well not necessarily mean that the ichthyoplankton survey sampled a larger part of the production, as sampling has been restricted to the upper part of the bottom water.

Despite these difficulties of interpreting egg production estimates, the high abundances of larvae in eastern spawning areas in the 1970's and also mid 1980's clearly indicate substantial egg survival success. A potential substantial drift of larvae from the Bornholm Basin into eastern spawning areas could not be confirmed by drift modelling studies (Hinrichsen *et al*., 2003). More likely is that the applied vertical distribution model based on data from vertical resolving net sampling in the Bornholm Basin underestimates the buoyancy of cod eggs produced in eastern spawning areas. A possible explanation may be that higher salinities at gonadal maturation and fertilisation affect the buoyancy of the eggs negatively. A validation of modelled vertical egg distributions in eastern spawning areas by vertically resolving net sampling was difficult, as at no occasion since 1996 cod eggs were present in the water column in sufficiently high numbers to fit a distribution. Applying an experimentally derived female size – egg buoyancy relationships using results from incubation experiments conducted at Gotland (Hjerne, 2003), i.e. at low salinities, resulted in rather similar low egg survival rates in eastern spawning areas, i.e. 0-15% in SD 26 and 0-6.5% in SD 28.

As larger females produce on average more buoyant eggs (Nissling and Vallin, 1996), a substantial changes in the spawning stock size/age structure will affect the vertical distribution of cod eggs, a process presently not considered in the vertical distribution model. Similarly a potential dependence of egg size on female condition is not considered. A decline in egg size with continuation of spawning

activity has been described for Baltic cod (Vallin and Nissling, 2000) as well as for other cod stocks (e.g. Trippel, 1998). First time spawners show in general a decrease of egg size right from the beginning of the spawning activity, while repeat spawners show a parabolic shape in egg size with a peak relatively early in the spawning season. In addition spawning activity of larger females starts earlier than of smaller ones (Tomkiewicz and Köster, 1999). In the present study, the vertical egg distribution was sampled in May and in July. In years classified as early spawning situations this represents peak and late spawning activity respectively, while in years classified as late spawning situations, this corresponds to early and peak spawning. This introduces a bias to higher buoyancy in late spawning years, but does as well not explain the low OES values determined in eastern spawning areas for the entire time series.

Our analysis is based on point estimates of hydrographic (RV) or average conditions (OES) and thus ignores meso-scale horizontal variability, which may in fact allow egg development in specific areas of the basins, while average conditions were unfavourable. For example are oxygen concentrations in the southern Gotland Basin in general more favourable than in the central basin (MacKenzie *et al*., 2000), and meso-scale horizontal variability in egg survival rates within the Bornholm Basin has been demonstrated as well (ICES, 2004).

Comparing the OES and field based egg survival rates determined in the Bornholm Basin revealed highly significant relationships, but indicate also other sources of egg mortality to be important. Other processes potentially affecting egg developmental success are: i) salinity dependent fertilisation rate (Westin and Nissling, 1991), ii) lethal impact of low temperature (Thompson and Riley, 1981) and iii) endogenous processes as chromosome aberrations during embryonic development (Kjørsvik, 1994), contamination by toxicants (e.g. Schneider *et al*., 2000), and endogene parasites (e.g. Pedersen and Køie, 1994). In the OES we considered only temperature, by assuming that cod eggs are not shed into cold water layers avoided by adults (D'Amours, 1993) and do also not float up into these layers. As water temperatures below 2°C are seldom encountered in Central Baltic Basins during spawning time (only in 3 out of 24 years), and are restricted to the intermediate water and the upper halocline with in general low cod egg concentration, the impact of the applied procedure is limited.

Egg predation

Cod egg survival depends as well on predation by clupeids, while predation by other planktivorous predators appears to be of limited importance (CORE, 1998). The estimated cod egg consumption by herring and sprat populations in the Bornholm Basin exceeded corresponding egg production rates in all spring and early summer dates 1990-1992, clearly demonstrating either an overestimation of the consumption or an underestimation of the production values. Consumption rates by the predator population as well as egg abundance and production estimates are based on a variety of assumptions in the estimation procedures. The diet composition of herring and sprat presented here is based on 5148 and 5908 investigated stomachs, relatively evenly distributed over sampling dates and covering 9 to 19 different stations in the Bornholm Basin during each survey, for further details see Köster and Möllmann (2000). There is presently no indication that this sampling scheme is unable to resolve intra-

and interannual variability in diet compositions of clupeids, especially as data from several cruises early and late in the spawning season from 1988 to 1995 exist, confirming the described trends (Köster and Möllmann, 2000).

To quantify daily rations, an exponential evacuation model is used (Köster and Möllmann, 2000), which appears to be well in agreement with findings of Jobling (1986), who suggested exponential evacuation for fish feeding on small particles, e.g. zooplankton. A similar evacuation rate of fish eggs and other prey organisms is assumed, which might be more problematic. A low proportion of fish eggs identifiable to species level indicates a rapid digestion beyond identification in sprat, but the remains of eggs can be identified after several hours of digestion, thus being in the order of magnitude determined for mesozooplankton prey. Therefore, the applied procedure appears to be more reasonable, than to model the evacuation of fish eggs on a number basis separately (Köster and Schnack, 1994).

A hydroacoustic survey conducted in May/June 1999 (STORE, 2003) revealed the sprat distribution pattern within SD 25 as derived from historical surveys in the 1980's (ICES, 1994) to be probably not valid at high population sizes encountered since the early 1990's. Assuming the 1999 hydroacoustic survey distribution to be representative for the entire time series, would in fact result in approximately 50% lower population cod egg consumption rates. An attempt to estimate the sprat population size in the Bornholm Basin with the daily egg production method (Kraus and Köster, 2004), confirmed the population estimate from the hydroacoustic survey and contrasted spatially down-scaled results from area dis-aggregated MSVPA runs (STORE, 2003). This indicates that applied sprat population sizes are overestimated, while for herring no such bias could be detected. Expressing predation pressure in relative terms as done in the present study does not account for an overestimation of sprat predation relative to herring. This implies that the relative predation pressure modelled for early spawning times may hold, though being still sensitive against shifts in distribution pattern over time, but that the predation pressure after shift of spawning time into summer may not be comparable. In consequence, a series of hydroacoustic surveys has been launched within the German GLOBEC project (Alheit, 2004) to resolve the spatio-temporal distributions of clupeids in the central Baltic throughout the production period.

The applied prey selection model, i.e. that daily ration by individual predators per standing stock of prey is linearly related to the predator/prey overlap, is limited to early spawning situations and describes the individual egg consumption for sprat better than for herring. Thus, revisiting of the model, considering also stomach content data becoming newly available, appears to be indicated. Furthermore, Wieland and Köster (1996) demonstrated that advanced egg stages are selected by clupeids, likely due to their better visibility, implying an importance of predation on egg survival beyond the statement: it is only eaten what is anyhow doomed to die due to unfavourable oxygen conditions.

With respect to an underestimation of the daily cod egg production, it should be noted, that although the PEP is significantly related to the realised egg production, the former is about twice as high as extrapolated average daily and determined seasonal production values from ichthyoplankton surveys (Kraus *et al*., 2002). This indicates an underestimation of the egg production derived by

ichthyoplankton surveys or an overestimation by the PEP, e.g. due to atresia. Another factor explaining the discrepancy between both production estimates may be a limited fertilization success. Even if not fertilized, eggs are probably preyed upon. How fast non fertilized eggs are sinking to the bottom is still unclear, but the limited abundance values determined in ichthyoplankton surveys indicate a rather fast loss in buoyancy. A further potential problem is an insufficient coverage of the spawning area by the ichthyoplankton survey, which appears to be unlikely, as cod eggs need salinities > 11 PSU to be neutrally buoyant, with conditions being only available in the covered central Bornholm Basin.

Despite all reservations and uncertainties described above, it can be stated that egg predation intensity by clupeids depends on the ambient hydrographic conditions, with stagnation enhancing the vertical overlap between predator and prey. In turn, favourable oxygen conditions release cod eggs from predation by clupeids. This explains why we detected relatively close relationships between modelled oxygen related egg mortality and egg predation intensity. Secondly, timing of spawning defines the major predator, with late spawning time enhancing the horizontal overlap with herring, but releasing from predation pressure by sprat. In this respect, the shift of the cod spawning season into summer has been an advantage, as stock sizes of herring declined throughout the 1980's and 1990's, while the sprat stock increased to a historic high in the mid 1990's (ICES, 2003).

From egg to the larval stage

Comparing egg and larval abundances as well as observed and modelled egg survival with larval abundances indicated high mortality rates during hatching or in the early larval stage during mid 1990's. While information on endogenous factors impacting on hatching success is limited, there are at least three different processes which can explain high mortality in the early larval stage: i) sub-lethal effects of egg incubation at low oxygen concentrations and/or direct effects of low oxygen concentrations on larval survival (Nissling, 1994), ii) predation by clupeids (Köster and Möllmann, 2000) and iii) food limitation and starvation (MacKenzie *et al*., 1996).

Experimental studies demonstrated that low oxygen concentration at egg incubation impacts on larval activity and that vertical migration into upper water layers is not started before day 4 after hatch (Rohlf, 1999). Hence, a significant impact of the environment within and below the halocline on larval survival can be expected, as Nissling (1994) demonstrated that low oxygen concentration has an impact on larval survival. Due to differences in buoyancy and minimum lethal oxygen concentrations in the egg and larval stage (Rohlf, 1999) it appears to be unlikely, that the oxygen related egg survival is a suitable measure of oxygen related survival probability of larvae. Thus, the affect of sub-lethal oxygen conditions on larval performance is presently not integrated in the modelled oxygen related egg survival. However, given the favourable hydrographic conditions within and below the halocline after the 1993 major inflow, it appears unlikely that sub-lethal oxygen effects during egg incubation or low oxygen concentrations in larval dwelling depths are responsible for the low larval survival in 1993-1996.

Although cod eggs are suffering from predation by clupeids, there is little evidence of a substantial predation on cod larvae (Köster and Möllmann, 1997). This can partly be explained by a limited vertical

overlap of prey and predator. Only newly hatched larvae concentrate in relatively high quantities within or below the halocline, where they are available as prey to herring and sprat aggregating in these water layers while feeding. However, herring do not feed on these small larvae, potentially due to a mis-match in size preference (CORE, 1998). Sprat occasionally prey on cod larvae, specifically in situations when they are attracted to fish larvae as prey by high abundances of sprat larvae in the plankton (Köster and Möllmann, 1997). For further discussion also in respect to a potential bias caused by rapid digestion times, see Köster and Möllmann (2000). With respect to low larval survival in 1993-1996, predation by sprat can be excluded as major process as the predator prey overlap was low, both vertically and seasonally. Oxygen concentrations allowed sprat to dwell in spring and early summer close to the bottom, while eggs hatched in the halocline and furthermore the major part of the cod egg production took place in summer, when sprat abundance is substantially lower (see above).

The impact of food availability on larval growth and survival has been tested by Hinrichsen *et al*. (2002b) with a coupled tropho/hydrodynamic model, considering explicitly temporal and spatial variability in prey species–stage distribution and physical environmental conditions in the Bornholm Basin. Results indicated the necessity of a match in calanoid nauplii and larval abundance in space and time to generate high survival rates of early larvae. In times of high reproductive success of *P. elongatus*, cod larval survival appears to be ensured, as there exists a perfect spatial match between nauplii and cod larvae, except for late spawned individuals. In contrast, in the absence of *P. elongatus* nauplii, late spawning and/or rapid transport into shallower areas with higher production of other calanoid copepod species is a pre-requisite for survival (Hinrichsen *et al.*, 2002b). A strong decline of *P. elongatus* standing stocks in the end of the 1980's and beginning of the 1990's, coupled to a decrease in salinity in the Central Baltic and thus also dependent on large scale atmospheric forcing conditions affecting the hydrography (Möllmann *et al.*, 2000, 2003), resulted in simulated low larval survival from main spawning activity in 1993-1995 and 1997. Low larval survival is confirmed for these years by observed and modelled late egg stage production and recruitment ratios. However, high simulated survival in 1996 could not be verified by observations.

Apart from various potential improvements in the trophodynamic IBM formulation and model parametrisation (see Hinrichsen *et al.*, 2002b for further discussion), the present coupled model approach has to cope with a relatively sparse temporal and spatial resolution of prey fields utilizing zooplankton data from the entire central Baltic. As spatial coverage has been more complete in eastern Baltic areas since 1985, this procedure may have biased the prey field to lower *P. elongatus* abundance, as salinities are generally lower in eastern Baltic basins. However, a statistical comparison of non-seasonal *P. elongatus* biomass anomalies in the different SDs did not give any indication for a significant difference between SDs, although the timing in peak biomass appears to be later in eastern areas (Möllmann *et al*., 2000). Newly available zooplankton data sampled in April, May, June and August 1999 in the Bornholm Basin confirmed the production period of *P. elongatus* to be in spring and early summer with reproduction areas being the deep Baltic basins (Hansen *et al*., 2004). *P. elongatus* nauplii showed highest concentrations in the upper 50m water column in spring and after

establishment of a warm surface layer in the intermediate water, while nauplii of other abundant copepods concentrate in the surface layer or in the thermocline. In contrast to *P. elongatus*, nauplii of other copepods are more abundant in slope areas of the basins and shallow water areas. This is partly caused by hatching from resting eggs deposited on oxygenated sediments and partly by distribution of the adult stock while reproducing (Dutz *et al*., 2004). In summary, the idealised prey field utilised in the coupled tropho/hydrodynamic modelling appears to capture the most prominent features in the spatial/temporal distribution of nauplii with and without *P. elongatus* present. From comparison of available nauplii abundance data (Krajewska-Soltys and Linkowski, 1994; Hansen *et al*., 2004) an underestimation of the food availability in the idealised prey field applied in the coupled modelling approach cannot be excluded, but for spring the deviation appears to be limited. Furthermore, all available data show a decline in prey availability, specifically *P. elongatus* from early to mid 1990's, confirmed as well by the HELCOM monitoring (HELCOM, 1996 and for more detail Dahmen, 1997).

A further test of the coupled tropho/hydrodynamic model output is possible by inspecting instantaneous protein growth rates from cod larvae (older than 6 days) sampled in the Bornholm Basin in May to July 1994 and May 1995 (Grønkjær *et al*., 1997). Compared with protein growth rates from experimentally reared cod larvae corresponding to poor, intermediate and good nutritional condition, 85 and 62% of the larvae caught in May 1994 and 1995 were classified to be in poor conditions, likely beyond the point of no return, and none and 15% in good condition. In June and July 1994 still more than half of the larvae were in poor condition, but an increased fraction of 20 and 37% were in good condition. Overall, these protein growth data suggests a substantial mortality of cod larvae in 1994 and 1995 and confirm an enhanced nutritional status of larvae spawned later in the season, as suggested by the coupled model output. Cod larvae sampled in 1999 in a situation with enhanced feeding potential (see above) are presently analysed for their nutritional condition.

Low larval survival in mid 1990's was indicated by the ratio of egg to larval abundance. However, the shift in cod spawning time may have resulted in a mis-match of high larval production and ichthyoplankton surveys in 1993 and 1994. Furthermore, no larval size or age data is available to compute larval mortalities in various years directly. Thus a validation of the simulated larval mortalities was possible by relating 0-group recruitment to different measures of surviving egg production only. Despite the general agreement of simulated and observed low larval survival in the mid 1990's, the relatively high larval survival suggested by the model for 1996 is not confirmed by any of the observations, while relatively high larval survival in 1999 is actually confirmed. Late spawning in combination with rapid transport into shallow water areas was of advantage for larval survival during mid 1990's, by this avoiding unfavourable feeding conditions caused by extremely low *P. elongatus* and below average abundances of other nauplii. As indicated by the model run for 1999, early spawning may have been a more successful strategy in most recent years, as nauplii abundances in spring and early summer showed an increasing trend, while abundances in the 3rd quarter were above average only in 1998.

From larval to juvenile stage

Significant relationships between larval abundance and recruitment at age 0 in SD 25 and 26 confirms a conclusion by Köster et al. (2003b), based on a shorter time series, that the later larval and early juvenile stage is less critical for cod recruitment than the egg and the larval stage. An insignificant relationship in SD 28 where regularly recruitment is encountered despite the absence of larvae in the ichthyoplankton surveys can be explained by i) drift of larvae from other spawning areas into the Gotland Basin, which according to drift simulations appears to be restricted from the Bornholm Basin (Hinrichsen et al., 2003), and ii) an immigration of juvenile cod as 2 year old from the coastal nursery areas in SD 26 as indicated by bottom trawl surveys conducted at different times of the year in the Gotland Basin (Plikshs, 1996).

MSVPA derived recruitment at age 1 and 2 compared fairly well to trawl survey results, especially in SDs 26 and 28 (Köster *et al.*, 2003b). However, the outstanding year-class strength 1979 was not confirmed by survey results. According to simulations by Neuenfeldt and Köster (2000), the application of constant suitability coefficients artificially inflates year-class strength 1979 and 1980 and underestimates the year-classes 1976 and 1977. In contrast, a significant impact of the suitability sub-model in use on the recruitment estimates in 1984 and 1985 could not be detected. Thus, the mis-match between high larval abundance and recruitment success in these years can presently not be explained by methodological problems in relation to the utilised MSVPA.

Studies on otolith microstructures suggest that surviving juveniles hatched late in the spawning season 1995 compared to the realised egg production and estimated peak larval production (St. John *et al*., 2000). Relatively high survival late in the spawning season has been related to a delay in peak zooplankton production, visible also in the available zooplankton data (see Fig. 13).

During the juvenile stage of demersal fish stocks, year class strength is regulated primarily by density-dependent processes mediated through competition for a limiting food resource and predation (Myers and Cadigan 1993). In fact evidence exist that growth of juvenile Baltic cod in shallow water areas may be affected by density dependent competition for food (Hüssy *et al*., 2003) and density dependent cannibalism (Uzars and Plikshs, 2000). Thus, transport to suitable nursery areas and away from concentration of adult cod may an important process governing juvenile growth and survival. Hinrichsen *et al*. (2003) investigated the drift of larvae and pelagic juveniles from the spawning area of the Bornholm Basin to nursery areas from 1986 to 1999 by combining 3-D hydrodynamic model simulations and spatial distributions of juvenile cod from 0-group surveys. The results suggest that juveniles caught in different areas of SD 25 can be assigned to different hatching times. Because of seasonal differences in the circulation pattern, southern coastal nursery areas are on average most important for early and late spawned individuals, whereas larvae hatching in June to mid July were on average transported towards the north or to a higher degree retained in the Bornholm Basin (Hinrichsen *et al*., 2003). This implies that the transport pattern and the importance of nursery areas have changed concurrent to the shift in spawning time. While in the 1980's and early 1990's northern nursery areas were of higher importance, transport to southern areas dominated in the remaining

period. Whether this general change in the transport regime has affected growth and survival of juveniles is unclear at present, and obvious next steps are studies on nursery habitat quality in terms of suitable prey availability and predator abundance.

Environmentally sensitive stock recruitment relationships

The stock recruitment models established here are based on earlier statistical models with different variables (Köster *et al.*, 2001a), containing for SD 25 besides the potential egg production corrected for egg predation, the oxygen content in the RV and a larval transport index, while for SD 26 and 28 the potential egg production and the RV were included as variables. These statistical models were fitted to time series covering 1976-1995 and were tested by Köster *et al*. (2003b) predicting cod recruitment in 1996-1999 as derived from area dis-aggregated MSVPA's as well as recruitment estimates from the Baltic International Trawl Survey. In the present models, the OES is used in all SDs to accommodate the impact of oxygen depletion on egg survival, simply by multiplication of OES with the potential egg production. The relative egg predation is excluded from the model in SD 25, as it is closely related to OES. The transport index representing the transport of larvae into suitable feeding environments was replaced by the product of nauplii availability and pursuit success, based on the results from the coupled tropho/hydrodynamic model output (Hinrichsen *et al*., 2002b). Adding additional physical variables to the relationships, i.e. an area specific upwelling index as a proxy for primary production and the BSI index (STORE, 2003), as proxy for transport from western to eastern spawning areas, did not improve the explained variance in recruitment, with none of the additional variables being significant.

The established statistical models explain a considerable part of the variability encountered in cod recruitment. The remaining variability may be due to a number of processes not included in the present exercise such as egg fertilization success (Vallin *et al*., 1999), the parental influence (age/size structure, condition) on egg (Vallin and Nissling, 2000) and via egg on larval characteristics (Nissling *et al.*, 1998), for further discussion see Köster *et al.*, (2001a). Other problems are apparent: i) to incorporate various factors affecting different early life stages in one model relating egg production by the spawning stock to subsequent recruitment (Rothschild, 1986), ii) to resolve the potential non-linearity and additive effects of different factors on subsequent early life stages and iii) to determine the historical recruitment originated by specific spawning components (e.g. Köster et al., 2001b).

The parameter estimates derived from the different statistical models indicate a higher influence of oxygen conditions on recruitment in eastern and northern spawning areas confirming substantial differences in oxygen related egg survival determined for the different basins (see above). However, one would expect that the parameter c becomes negative in an additive model indicating the existence of a critical threshold in the production of surviving eggs below which recruitment becomes zero. This is not the case, which means that at sufficiently high prey availability, compensating for the negative intercept, predicted recruitment is positive despite zero egg survival. In this respect a multiplicative model may be more appropriate. Köster et al. (2001a), fitting such a simple multiplicative model, concluded that although the model explained more of the variance in recruitment in SD 26 and 28, it

did not exhibit better predictive power, but consistently underestimated recruitment at high reproductive success. Having simplified the model structure here to a direct measure of oxygen related egg survival and secondly larval survival in relation to food availability assumed to be an asymptotic relationship, may suggest a multiplicative model of the following type to be more plausible: $R = a * \sum (PEP_i * OES_i) * (1-\exp (-c * T * P_{p \text{ or } n}))$.

Impact of hydroclimatic conditions on Eastern Baltic cod stock dynamics

The decline of the Eastern Baltic cod stock during the 1980's and early 1990's was caused by a substantial reduction in reproductive success in combination with increasing fishing pressure (Köster *et al*., 2003a). The decline in reproductive success was mainly driven by: i) anoxic conditions in deep water layers of important spawning sites causing high egg mortalities, ii) high egg predation by clupeid predators in the only productive spawning area of the Bornholm Basin and iii) to a lesser extend juvenile cannibalism at high adult stock size. Limited larval survival caused by food limitation in combination with increasing fishing mortalities after relaxing severe management measures enforced in 1993, explains the lack of stock recovery of the stock in mid 1990's. In contrast, favourable oxygen and salinity conditions in the 2nd half of the 1970's in combination with moderate fishing mortalities explains the increase in stock size to historic high levels in the beginning of the 1980's. Despite of our improved understanding of processes affecting the recruitment of the Eastern Baltic stock, quantification of relationships and especially prediction of future recruitment remains difficult as various processes are interacting and non-linear responses likely.

The intensity and significance of these processes are in one way or the other forced by ambient hydrographic conditions related to the overall climatic regime over Northern Europe, prevailing westerly weather with strong westerly winds resulting in mild winters and above normal rainfall since mid 1980's (e.g. Hänninen *et al*., 2000). The most prominent trends are declining salinities due to enhanced river run-off and precipitation as well as lack of major Baltic inflows, higher than normal temperatures in the intermediate and the bottom water – also the latter affected by winter air temperatures, and declining oxygen concentrations caused by i) the lack of major inflows, ii) lower oxygen solubility at higher temperatures and iii) high oxygen consumption rates due to above average temperatures (Hinrichsen *et al*., 2002a; MacKenzie *et al*., 1996; ICES, 2004). Declining salinity and oxygen concentrations affect cod egg survival directly and indirectly via the enhanced overlap between clupeids and cod eggs as prey. There exist as well indication that low oxygen concentration at egg incubation affects additionally larval activity and survival (Rohlf, 1999).

As described by MacKenzie and Köster (2004) sprat recruitment is significantly related to temperature conditions in the Baltic deep basins. Sprat is a major prey species of cod and prey availability affects fecundity (Kraus *et al*., 2002) and likely also growth and maturation, by this influencing cod recruitment positively. On the other hand sprat acts as predator on cod eggs and feeds intensively on *P. elongatus* in spring (Möllmann and Köster, 2002), with the latter process contributing to the decline of the most important prey species for early larval cod. In summary, the interactions between cod and sprat are complicated, but it appears to be likely that a warmer thermal regime favours rather sprat than cod

reproduction, thus stabilising the present sprat dominated system in the Central Baltic (Köster *et al*., 2003a).

The shift in the overall hydroclimatic regime had as well an impact on the zooplankton abundance and species composition. *P. elongatus* standing stocks declined in parallel to salinities, a trend even continuing for some years after the 1993 major Baltic inflow (Möllmann *et al*., 2004). Furthermore, higher temperatures favour *Acartia* spp. and *Temora longicornis* production (Möllmann et al., 2000, 2003), both euryhalin and important prey species for different life stages of sprat (Voss *et al*., 2003; Möllmann and Köster, 2002). In summary, also the encountered changes in the meso-zooplankton community are of benefit for sprat but not for cod reproduction.

A shift in main spawning time of cod from spring to summer - with the processes acting still not completely understood (Wieland *et al*. 2000a), reduced the egg predation pressure by sprat and enhanced the larval prey availability in the absence of *P. elongatus*. Furthermore, it appears likely that enhanced wind driven transport late in the spawning season (Hinrichsen *et al*., 2003) reduces the horizontal overlap between juvenile and adult cod and together with late settling of juveniles, i.e. after the main adult feeding period, results in low cannibalism intensity. In terms of optimising egg and larval survival in relation to the oxygen conditions, early spawning is the more successful strategy, due to deteriorating conditions throughout the year (MacKenzie *et al*., 2000).

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Tables

Tab. 1 Daily mortality rates from egg stage I to III in different spawning areas in years with contrasting environmental conditions, i.e. 1974, 1976 and 1989 (April to June) and 1995 and 1996 (July/August).

Year	Bornholm Basin	Gdansk Deep	Gotland Basin
1974	0.272	0.122	0.164
1976	0.051	0.247	0.524
1989	0.191	1.247	1.217
1995	0.268	-	1.041
1996	0.199	-	1.322

Tab. 2 Parameter estimates and their significance levels, r^2 values and Durban Watson (DW) statistics of stock recruitment (age 0) relationships (multiple linear regression), PEP: potential egg production, OES: oxygen related egg survival, P_p: *P. elongatus* nauplii abundance, P_n: calanoid nauplii abundance and T: pursuit success.

SD	parameter estimates			p-levels for variables				r^2	DW*
	intercept	b	c	Intercept	b	c (P_p*T)	c (P_n*T)		
25	$-5.5850*10^7$	0.00002090	51898	0.648	0.021	<0.001		0.69	1.35
26	$-4.9723*10^7$	0.00009135	29217	0.438	0.012	0.001		0.73	0.71
28	$-4.4356*10^7$	0.00105845	21646	0.394	0.035	<0.001		0.67	1.26
25	$-4.2372*10^7$	0.00002014	20729	0.692	0.014		<0.001	0.75	1.24
26	$-3.2387*10^7$	0.00009186	10810	0.606	0.013		<0.001	0.72*	0.68
28	$-5.0136*10^9$	0.00130917	8165	0.26	0.006		<0.001	0.71*	1.06
all model 1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.78	n.a.
all model 2	$-2.4103*10^8$	0.00003939	105836	0.292	0.010	<0.001		0.73*	1.15
all model 2	$-1.9701*10^8$	0.00003889	40723	0.355	0.008		<0.001	0.76*	0.97

* Indications of autocorrelation in the residuals (DW < 1.2)
n.a.: not applicable

Figures

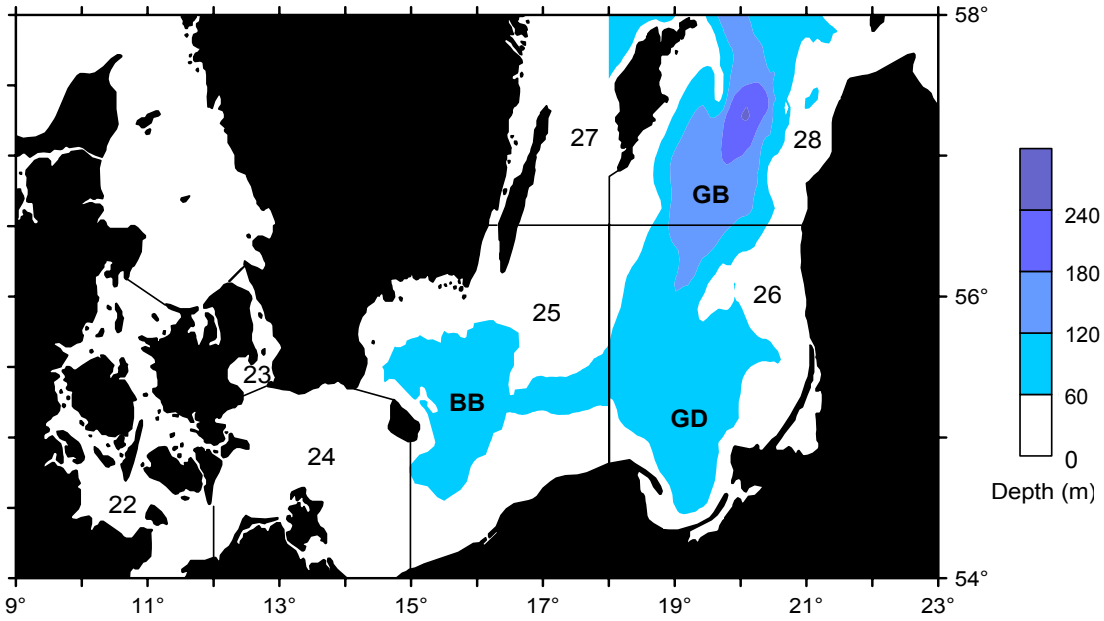

Fig. 1 The southern and central Baltic with spawning areas of the eastern Baltic cod stock in ICES SD 25 (BB: Bornholm Basin), 26 (GD: Gdansk Deep) and 28 (GB: Gotland Basin).

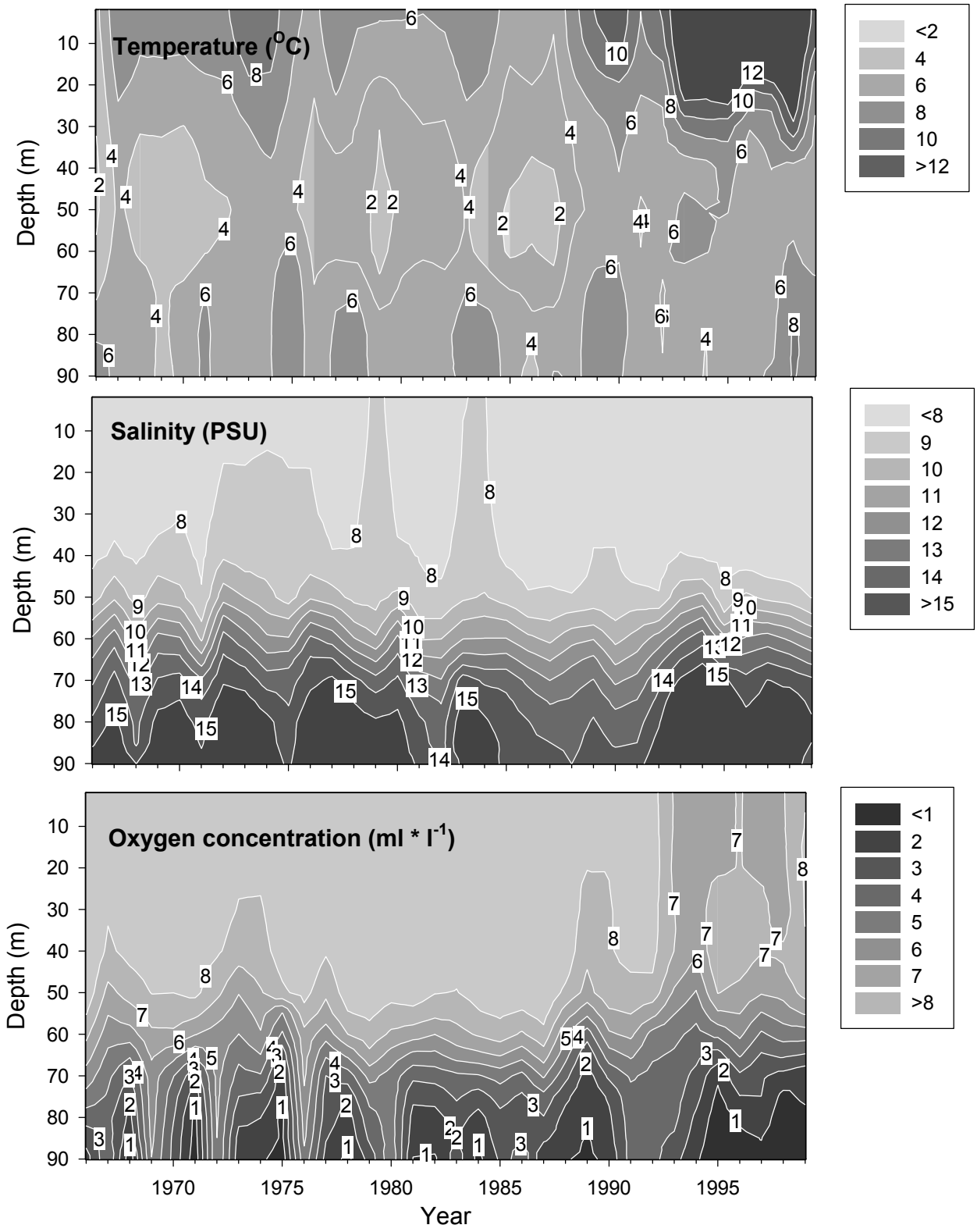

Fig. 2 Temperature, salinity and oxygen concentrations during main spawning time (2nd quarter 1966-1989 and 3rd quarter 1990-1999) in the Bornholm Basin (SD 25).

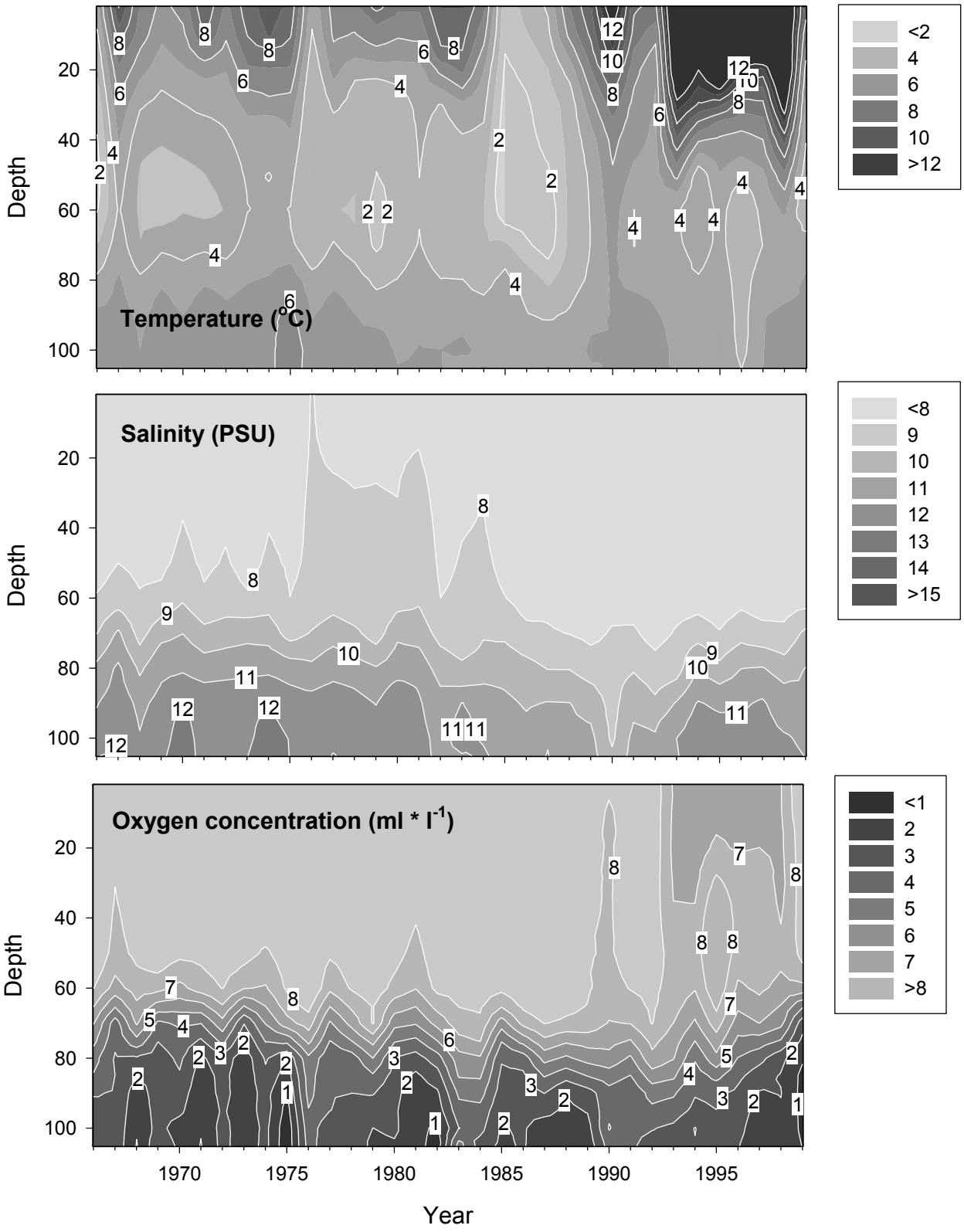

Fig. 3 Temperature, salinity and oxygen concentrations during main spawning time (2nd quarter 1966-1989 and 3rd quarter 1990-1999) in the Gdansk Deep (SD 26).

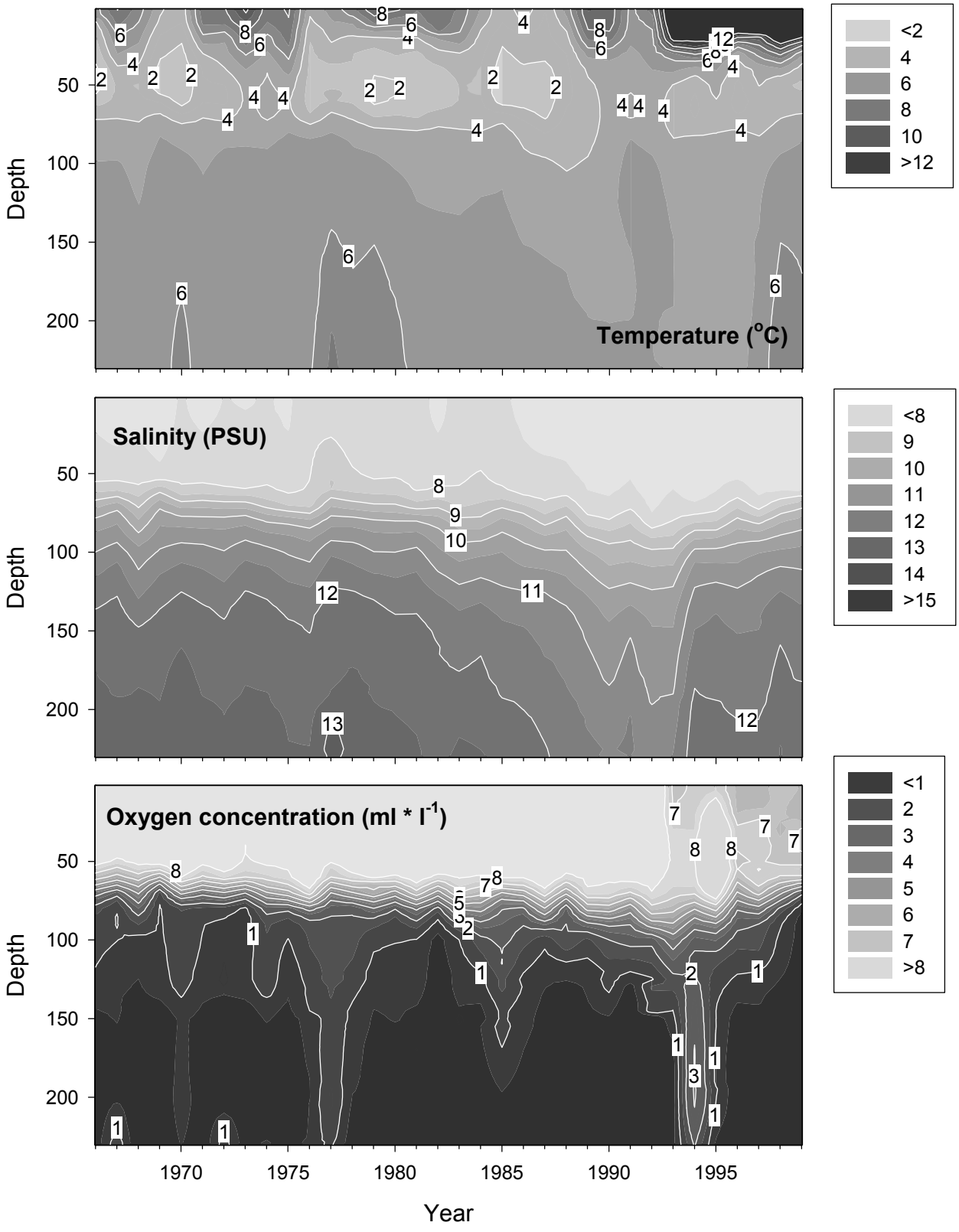

Fig. 4 Temperature, salinity and oxygen concentrations during main spawning time (2nd quarter 1966-1989 and 3rd quarter 1990-1999) in the Gotland Basin (SD 28).

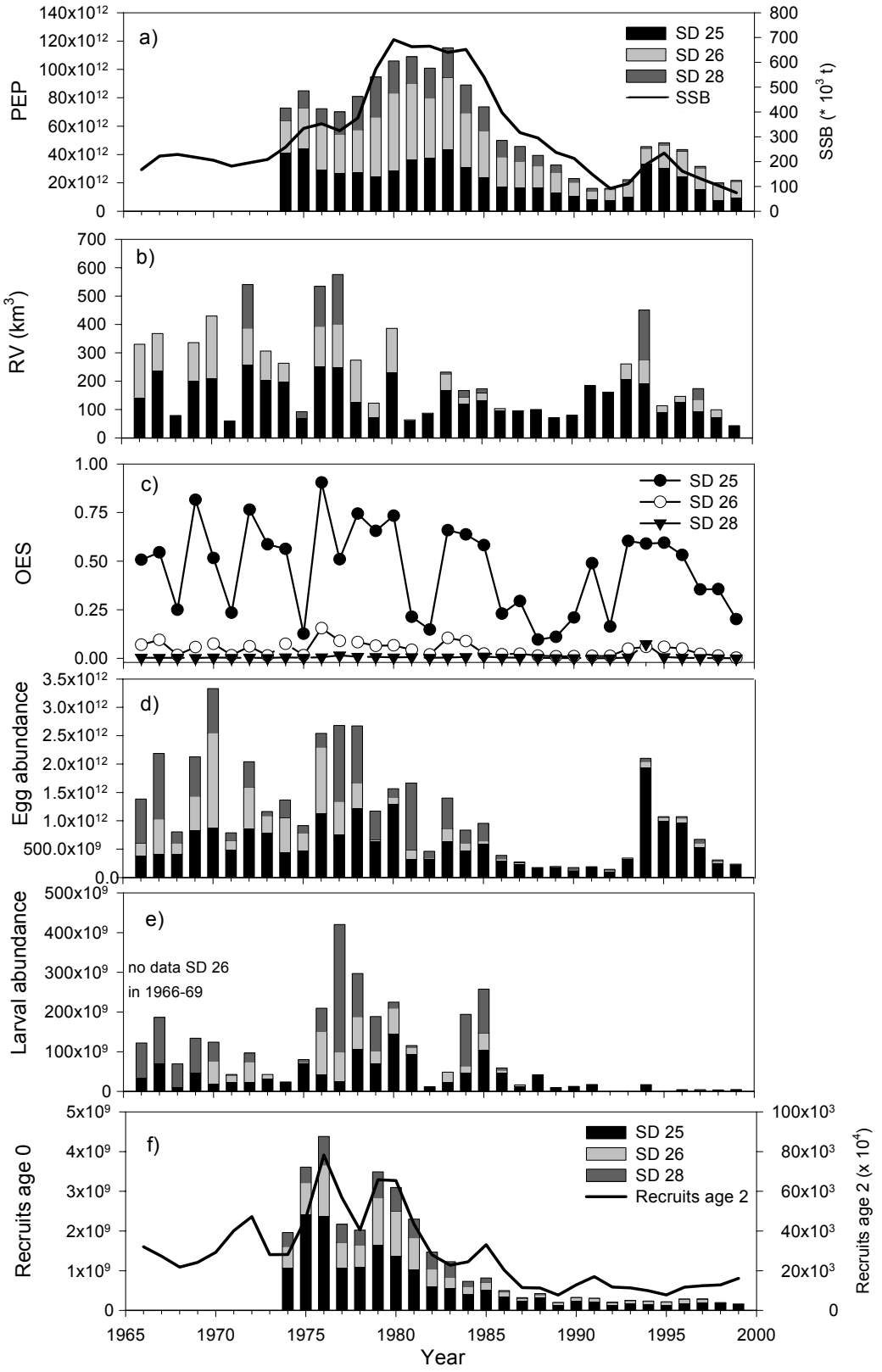

Fig. 5 Time series of a) spawning stock biomass (SSB) and potential egg production (PEP), b) reproductive volume (RV), c) oxygen related egg survival (OES), d) egg abundance, e) larval abundance and f) recruitment at age 0 in SD 25, 26 and 28 or the entire central Baltic (SSB and recruits at age 2).

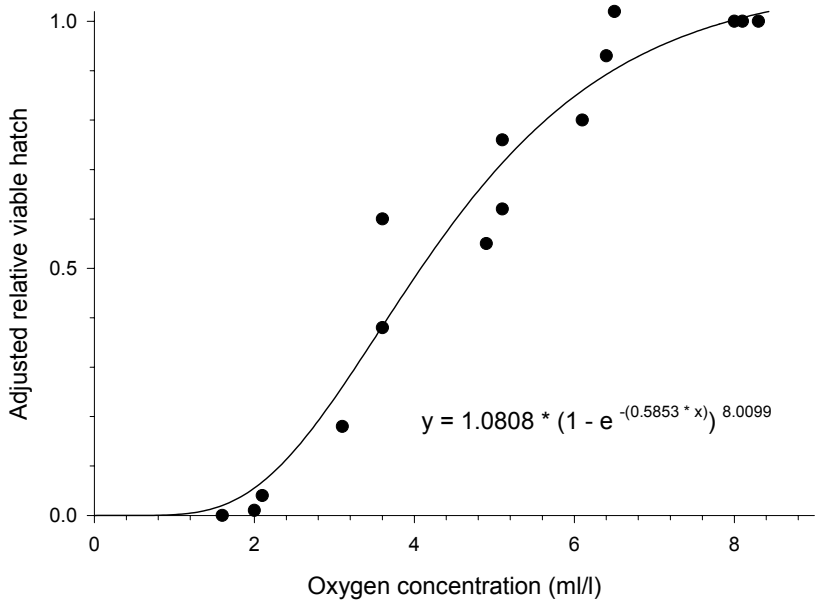

Fig. 6 Relative viable hatch of cod eggs at different levels of oxygen concentration during egg incubation adjusted to survival at normoxic conditions.

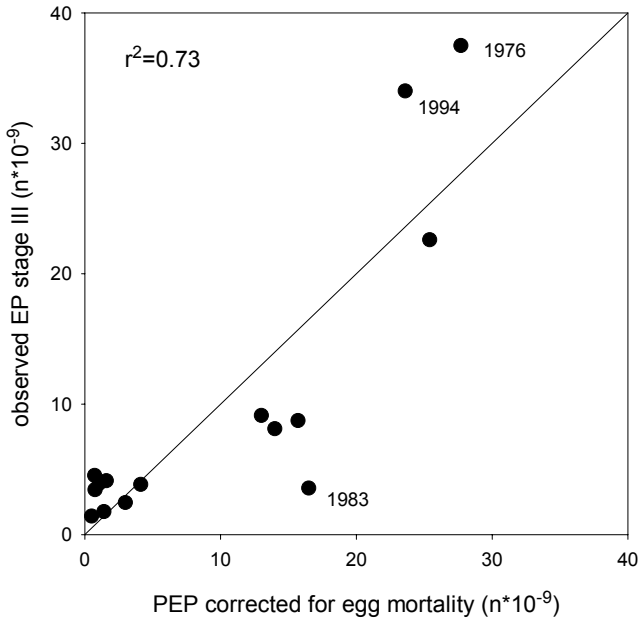

Fig. 7 Linear regression of daily production of cod egg stage III (EP) in the Bornholm Basin on potential egg production (PEP) corrected for oxygen related egg survival.

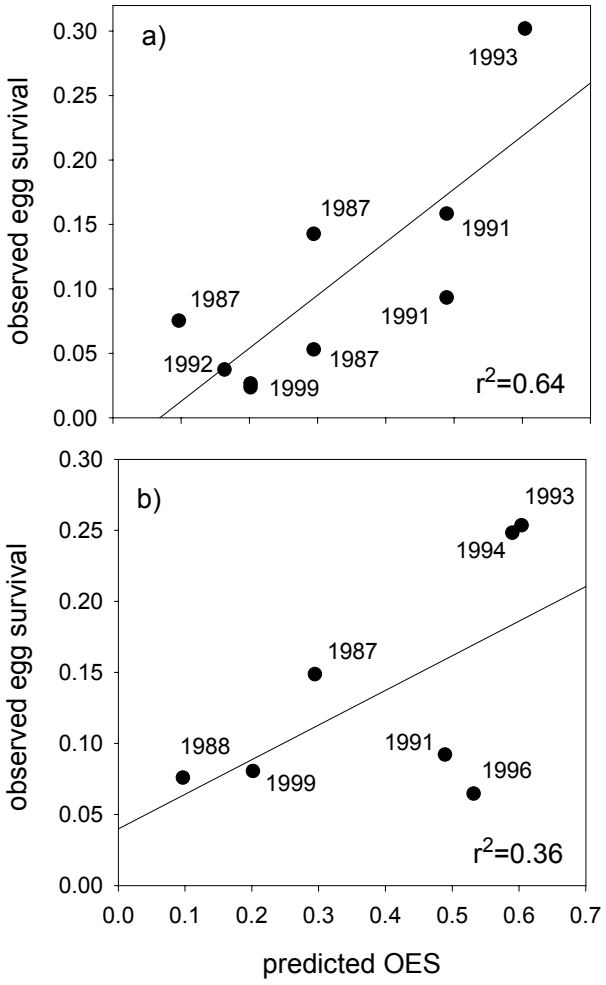

Fig. 8 Observed egg survival (proportion surviving to stage III) from following cohort development (a) and from seasonal stage specific egg production curves (b) vs. predicted oxygen related egg survival (OES).

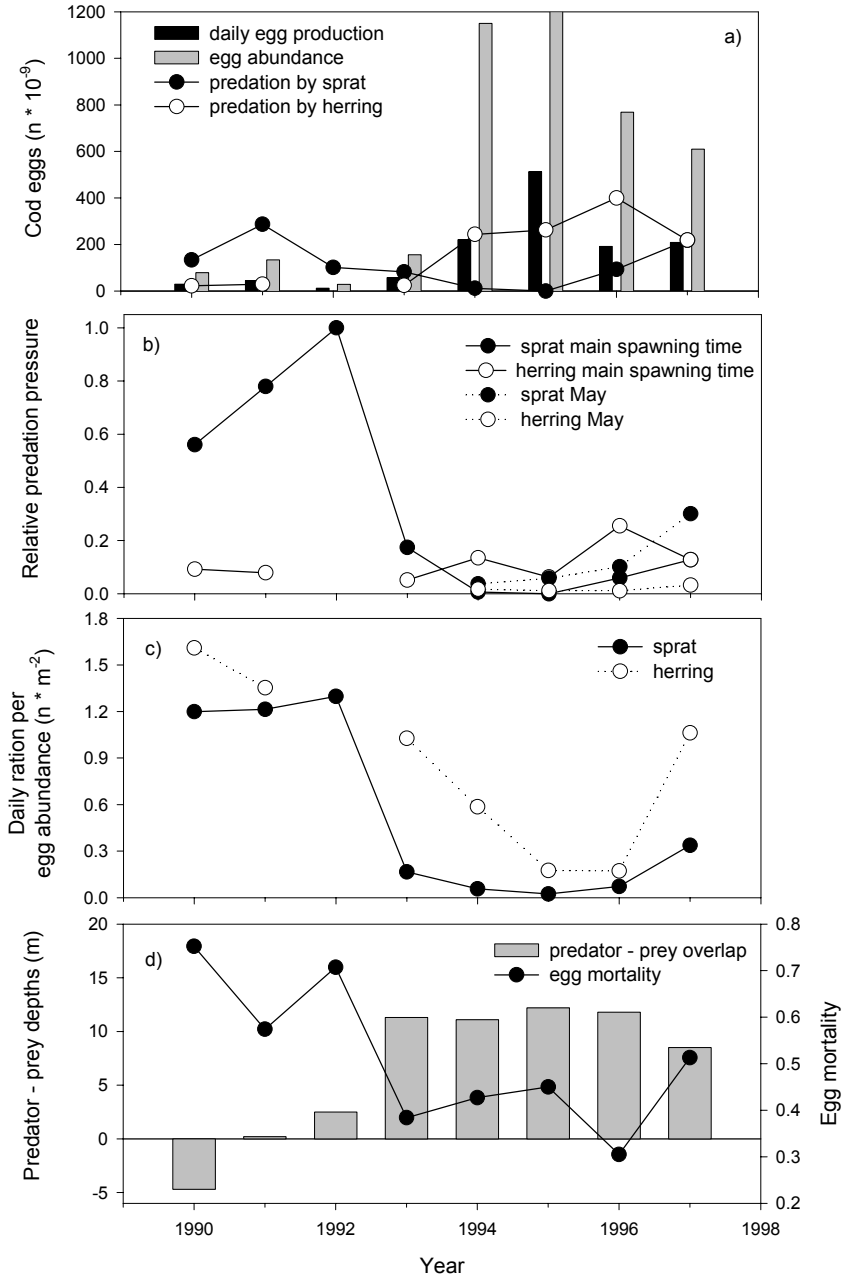

Fig. 9 Daily cod egg consumption by clupeids in the Bornholm Basin during main spawning periods in comparison to daily production rates and standing stocks of eggs (a); corresponding relative predation pressure (b); daily ration by individual sprat and herring per egg abundance (c); spatial overlap between predator and prey and cod egg mortality based on vertical resolving ichthyoplankton and hydrography sampling during stomach sampling cruises (d).

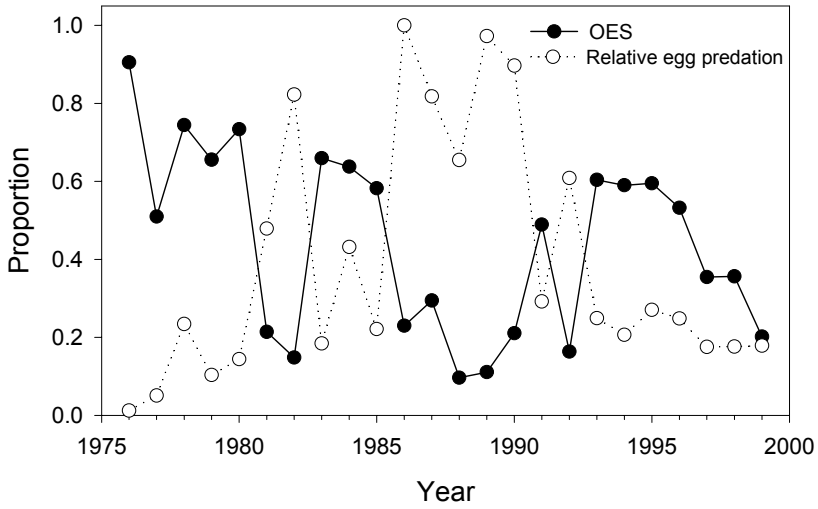

Fig. 10 Modeled relative egg predation by clupeids in the Bornholm Basin and oxygen related egg survival (OES) during main spawning periods.

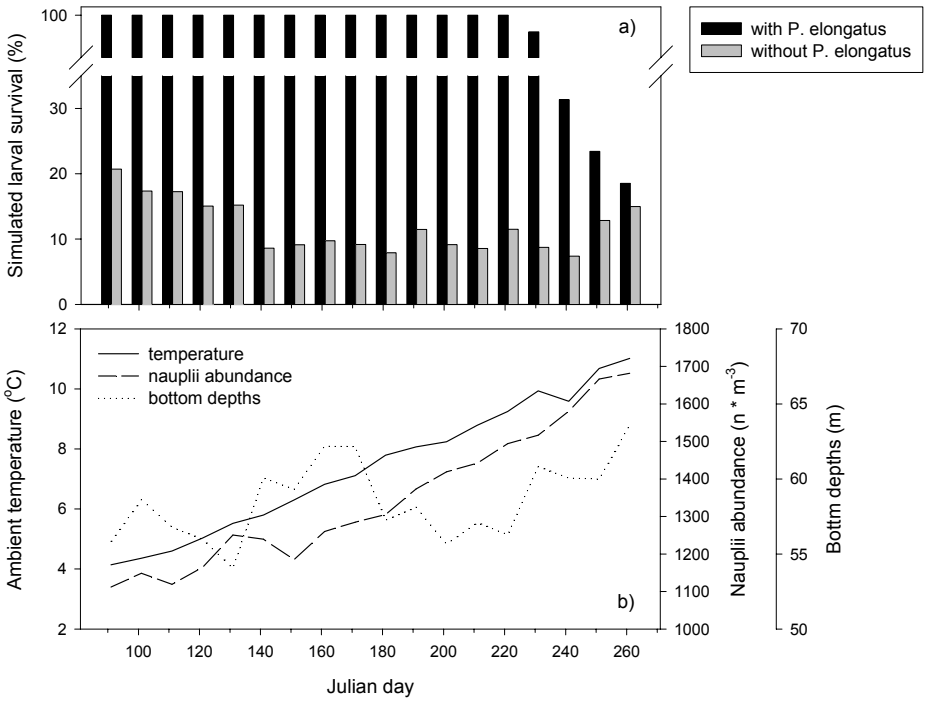

Fig. 11 Seasonal variability in simulated larval survival (averaged 1986-1999) in SD 25 from coupled tropho/hydrodynamic model based on idealized prey field, with and without *P. elongatus* (a) and average ambient environmental variables encountered by surviving larvae (runs without *P. elongatus*), i.e. nauplii abundance, temperature and bottom depth after drift period as a measure of transport (b), modified after Hinrichsen et al., (2002a).

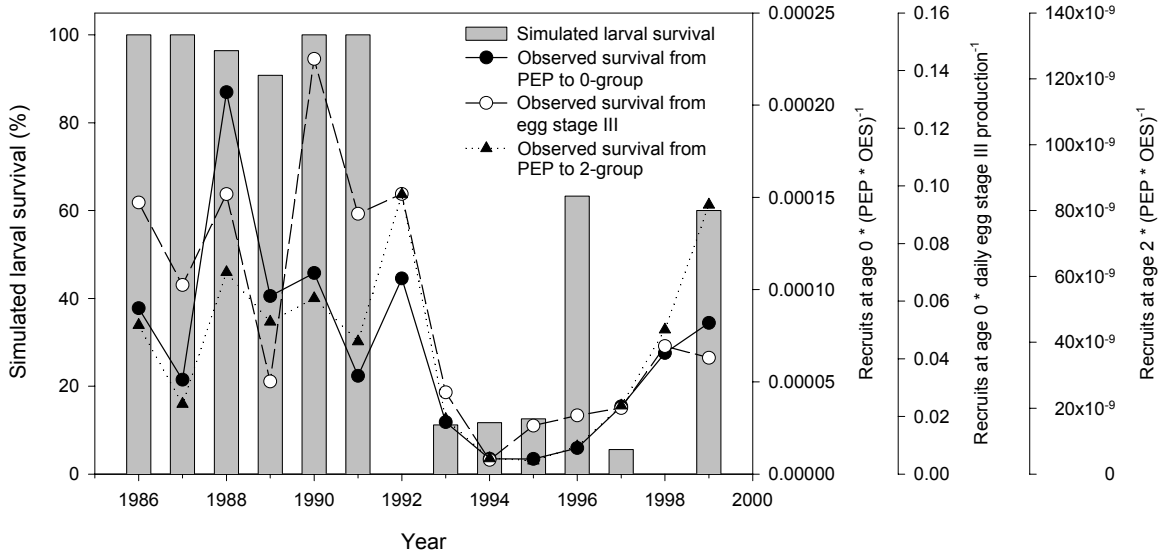

Fig. 12 Interannual variability in simulated larval survival in SD 25 from coupled tropho/hydrodynamic model based on idealized prey field, with exception of 1999 based on observed zooplankton abundance; measures of larval survival as recruits at age 0 per surviving egg production (PEP times OES) and per observed average daily egg stage III production as well as recruits at age 2 in the entire eastern Baltic per sum of surviving egg production in each SD (PEP times OES).

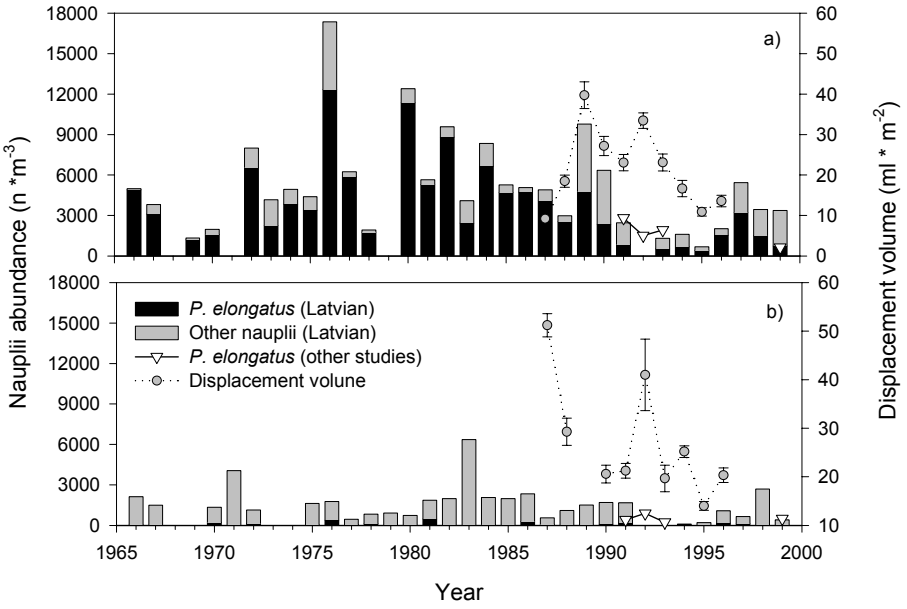

Fig. 13 *P. elongatus* and other nauplii abundance (whole water column) in SD 26 and 28 in the 2nd (a) and 3rd quarter (b) from Latvian monitoring (no data available in the 2nd quarter in 1968, 1971, 1979 and 1992 and in the 3rd quarter in 1968-69, 1972-73 and 1992-93), in SD 25 from Polish studies in 1991 to 1993 (water samples) and STORE in 1999 (50um net), and zooplankton displacement volume +/- standard error (335 um Bongo samples).

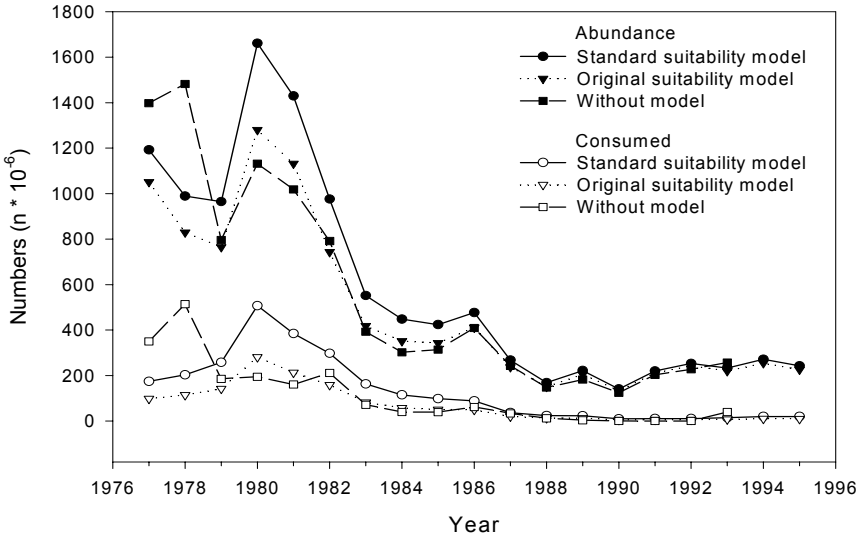

Fig. 14 Juvenile cod (age-group 1) abundance and consumption (cannibalism) estimated by MSVPA runs with the standard suitability model implemented in the Baltic, the original model suggested by Gislason and Sparre (1987) and without suitability model, modified after Neuenfeldt and Köster (2000).

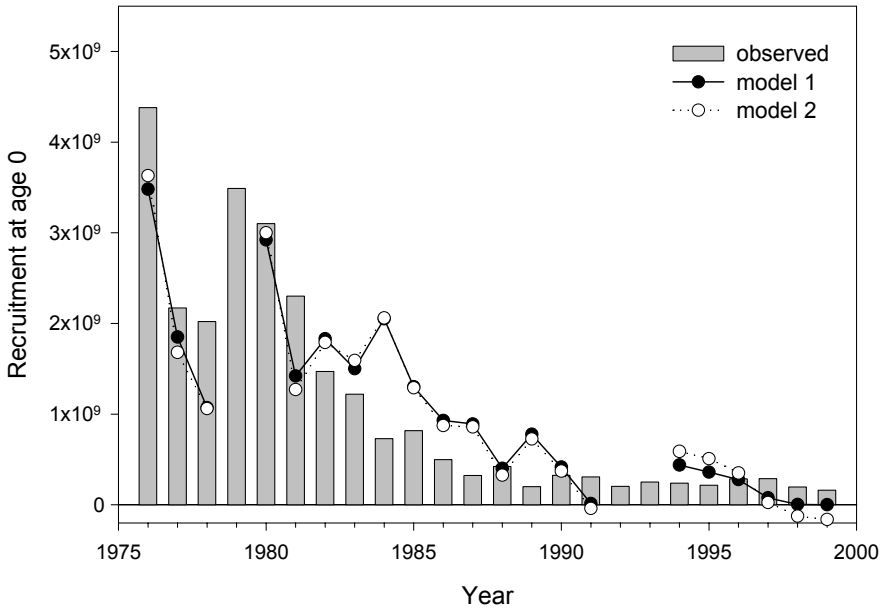

Fig. 15 Observed and predicted recruitment (age 0) based on multiple linear regression models for each SD incorporating PEP * OES and T * P_p as additive variables, fitted to different SD and subsequently integrated over areas (model 1) and fitted to all SD at once (model 2).